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The biology and control of the American Whelk Tingle *Urosalpinx cinerea* (Say) on English oyster beds

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The biology and control of the American Whelk Tingle *Urosalpinx cinerea* (Say) on English oyster beds

I. INTRODUCTION

THE American whelk tingle, drill or borer, *Urosalpinx cinerea* (Say), originated in Britain from the United States, where it is said to be one of the worst enemies of the oyster (Glancy, 1953). It is a gastropod mollusc of the family Muricidae, represented also in this country by *Nucella* and *Ocenebra*. Of these, *Ocenebra* is no longer present in the oyster-producing areas on the East coast (Mistakidis and Hancock, 1955), but is an active enemy of oysters on the South coast. *Nucella* is of widespread occurrence, but there is no evidence that it is of importance in oyster culture. *Urosalpinx* has gradually increased in this country during this century, and serious damage to oyster cultivation has already been recorded (Orton and Winckworth, 1928; Cole, 1942; Hancock, 1954). This further study of the habits of *Urosalpinx* was undertaken with a view to producing control measures and limiting its distribution.

II. DISTRIBUTION

1. HORIZONTAL DISTRIBUTION

ORTON and Winckworth (1928) believed that *Urosalpinx* was introduced into Britain with consignments of oysters from America at about the same time as *Crepidula fornicata* (L.), i.e. at about 1880. The earliest record of its occurrence, however, is that by Orton (1930) who first observed it in 1927 when studying native drills, and subsequently discovered specimens in material preserved in 1920. Carriker (1955) has summarised the work of many authors on the distribution of *Urosalpinx*, and his detailed account shows that it is now present on the east coast of the United States of America from Maine to Florida, and in Washington and California on the west coast, and also in British Columbia, Western Canada. Needler (1941) recorded *Urosalpinx* from New Brunswick, Eastern Canada. There are no records of *Urosalpinx* in the oyster-producing areas of Holland, Belgium, France, South Africa, Australia or Japan (Carriker, 1955).

In England, the two main centres of distribution are believed to have been Brightlingsea and West Mersea, Essex (Cole, 1942), where for many years American oysters were relaid, and spreading from these centres it became abundant in the Rivers Blackwater and Colne and their creeks. Cole found that it occurred sparingly in the River Crouch and more abundantly in the River Roach and creeks around Paglesham, and suggested that it had been introduced not long before 1934. Recent surveys have shown that *Urosalpinx* is still present throughout the River Blackwater (G. D. Waugh, personal communication) and the River Colne. In the Rivers Roach and Crouch *Urosalpinx* is now abundant in both rivers, concentrations of up to 6,000 per acre being recorded in the River Roach, and up to 10,000 per acre in the River Crouch. This demonstrates a remarkable increase in density in the past fifteen years in the River Crouch, where *Urosalpinx* is now present on grounds up to 14 miles from the mouth of the river. An investigation of areas north of the River Colne has failed to reveal its presence in the Orford River, River Orwell or Hamford Water, areas where American or Essex oysters have previously been relaid, but showed that a small amount of migration has occurred northward along the coast from the River Colne as far as

Fig. 1. *Map showing the known distribution (darkened areas) of* Urosalpinx cinerea *(Say) in England.*

Frinton-on-Sea (Fig. 1). *Urosalpinx* was collected from the shore at L.W.O.S.T. (low water of ordinary spring tides) at Clacton, Holland-on-Sea and Frinton, but not at Walton-on-the-Naze. Enquiries and dredging in the River Medway have failed to disclose any traces of *Urosalpinx*. A small extension of the distribution on the Kentish flats at Whitstable, recorded by Cole (1942), was found by dredging, when tingles and spawn were taken as far east as Herne Bay Pier. Cole had suggested that *Urosalpinx* may not thrive on the Whitstable beds, where the bottom is hard and open to the sea. Although large numbers are not found there, such conditions do not seem to form a barrier to migration at Whitstable or on the Essex coast, but movement has been very slow. An intensive search has been made in areas on the South coast in which Essex or American oysters have been laid, but no *Urosalpinx* have been taken during surveys of Emsworth, Chichester, or Langstone harbours, or of the Salcombe estuary, Devon.

2. VERTICAL DISTRIBUTION

In the United States, *Urosalpinx* occupies a relatively broad vertical range from the mid-intertidal zone to unknown depths (Carriker, 1955). The greatest depth at which *Urosalpinx* has been taken is at 120 ft. off North Carolina (Chestnut, *cit.* Carriker, 1955). In England *Urosalpinx* is confined to an area with depth rarely exceeding 12 m. at L.W.O.S.T. Where it is found in open water with adjacent deeper channels, as at Whitstable, it has only been recorded in depths of a few metres.

The vertical distribution of *Urosalpinx* in the Rivers Roach and Crouch was studied on the shore and by dredge surveys throughout the year. In 1953 at the Common Shore (Figs. 2 and 7), a stretch of shore 100 m. in length was marked on the north side of the River

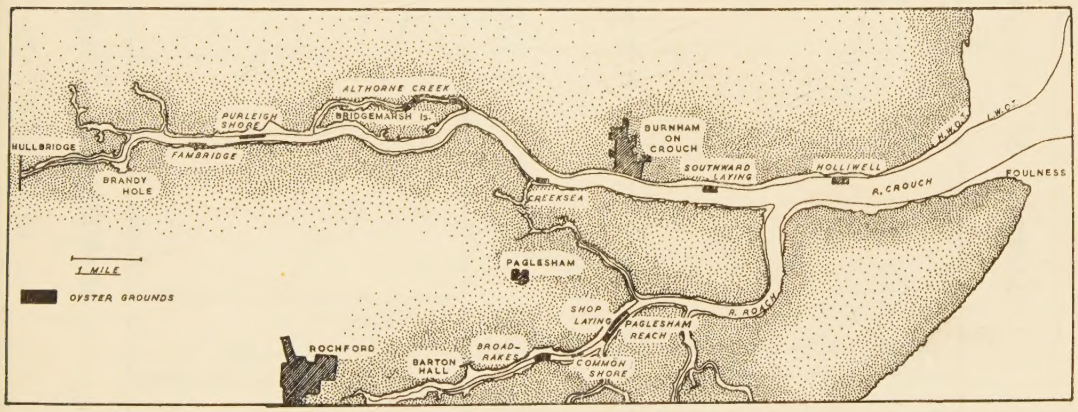


Fig. 2. *Map showing the oyster grounds in the Rivers Roach and Crouch, Essex, mentioned in the text.*

Roach and the area subtended by this base line across the river was divided by buoys into lanes 10 m. wide, parallel to the shore. The same area of ground was later used for a grab survey (Stations I, II, A–F, Fig. 7). Parallel dredge hauls, one in each lane, were made throughout the summer, using two 4 ft. 6 in. power dredges, and the numbers of *Urosalpinx* and spawn capsules taken were recorded. The results are shown in Fig. 3. The south bank of the river was of soft mud, so that dredge hauls were continued only as far as 100 m. below L.W.O.S.T., but the dredged ground included the deepest part of the river ($3\frac{1}{4}$ m. at L.W.O.S.T.). Throughout the year the majority of tingles and spawn were taken within 40 m. from L.W.O.S.T. Most tingles were dredged in May and June, and this is believed to be due to increasing activity as a result of rising temperature, coupled with a shoreward migration associated with spawning. This migration is discussed on page 15. Examination of the shore showed that tingles and spawn were found in the intertidal zone up to 50 m.

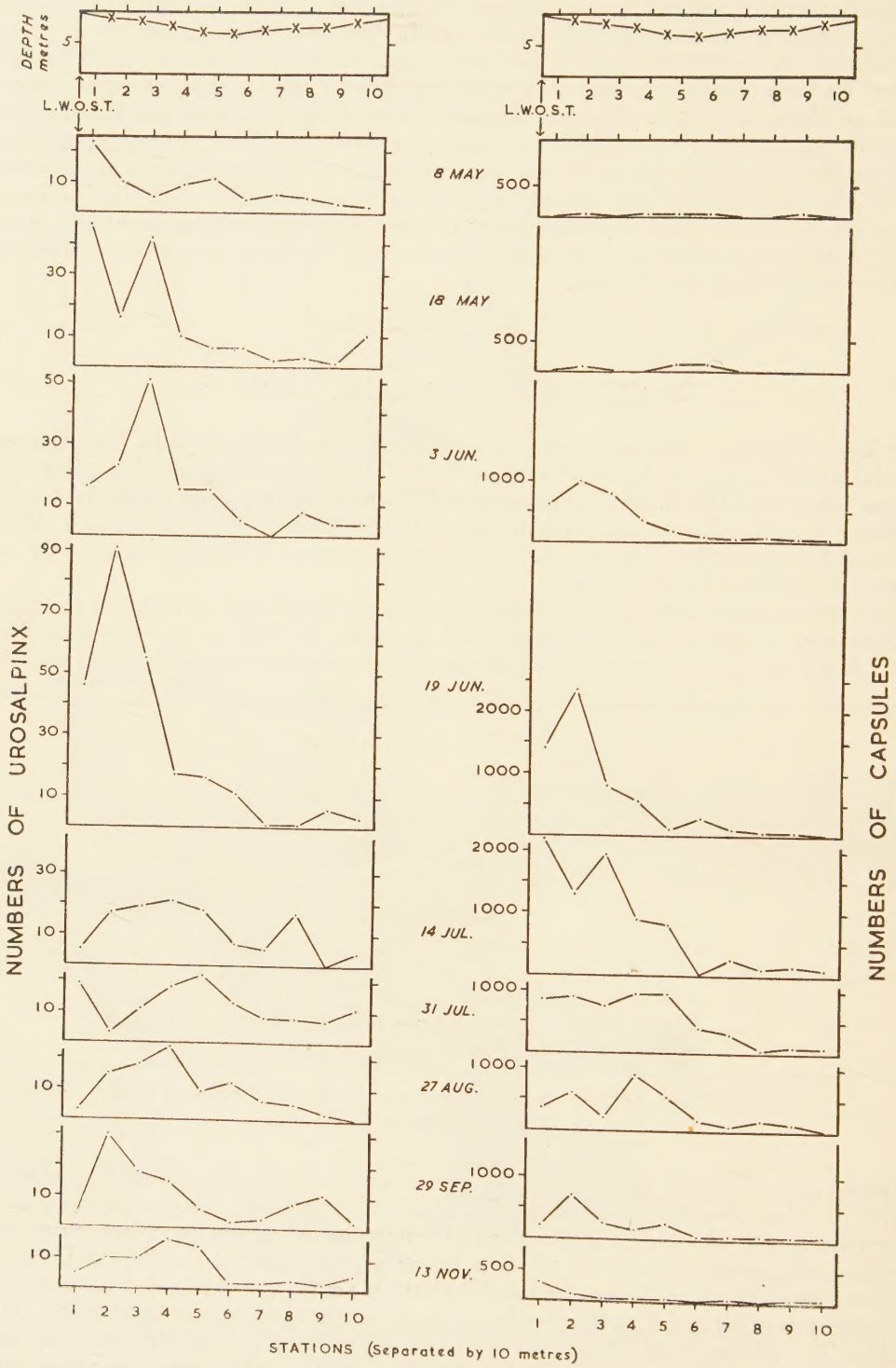


Fig. 3. *Numbers of* Urosalpinx *and its capsules taken in standard parallel hauls with two 4 ft. 6 in. power dredges over* 100 *m. at the Common Shore, River Roach, in* 1953. *A section across the river showing mean depths is given.*

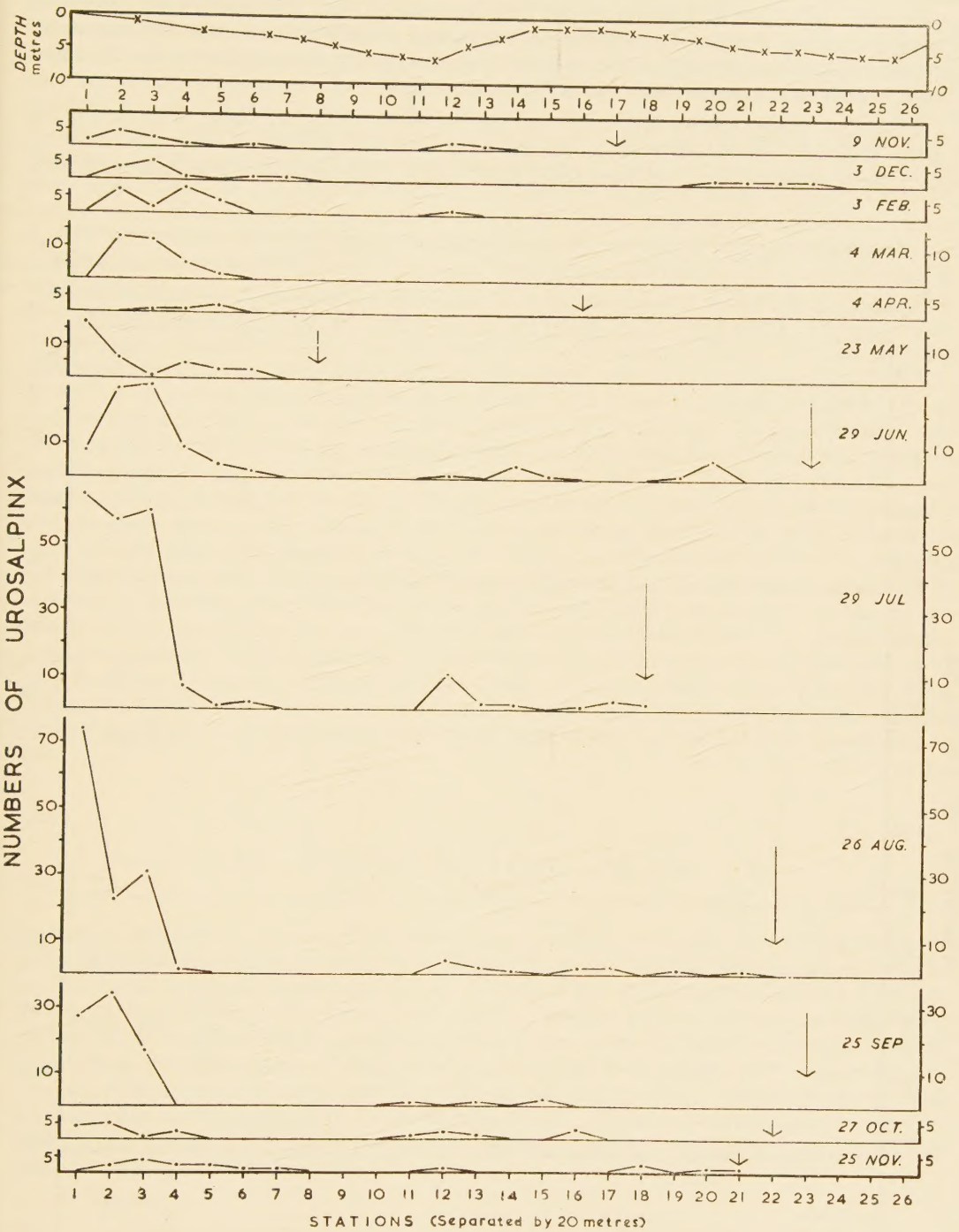


Fig. 4. *Numbers of* Urosalpinx *taken in standard parallel hauls with two* 4 *ft.* 6 *in. power dredges over* 125 *m. at the Southward Laying, River Crouch, November* 1954–55, *commencing* 10 *m. from L.W.O.S.T. on the north shore. A section across the river showing mean depths is given. The final dredge station on each date is indicated by an arrow.*

from L.W.O.S.T., that is with about 40% exposure. A few were found buried in mud under large rocks in this situation on the 19th November, 1954, and again in the following spring, suggesting that this distribution was not related exclusively to a spawning migration. Extensive migration of tingles on to the shore occurs during the summer at the Common Shore, which slopes gently from below low-water-mark.

A similar dredge survey was made on the Southward Laying, River Crouch Fig. 2) during 1954–55. Here the river is much wider, and dredge hauls were made at 20 m. apart, the first being 10 m. offshore from L.W.O.S.T. This area, too, was later used for a

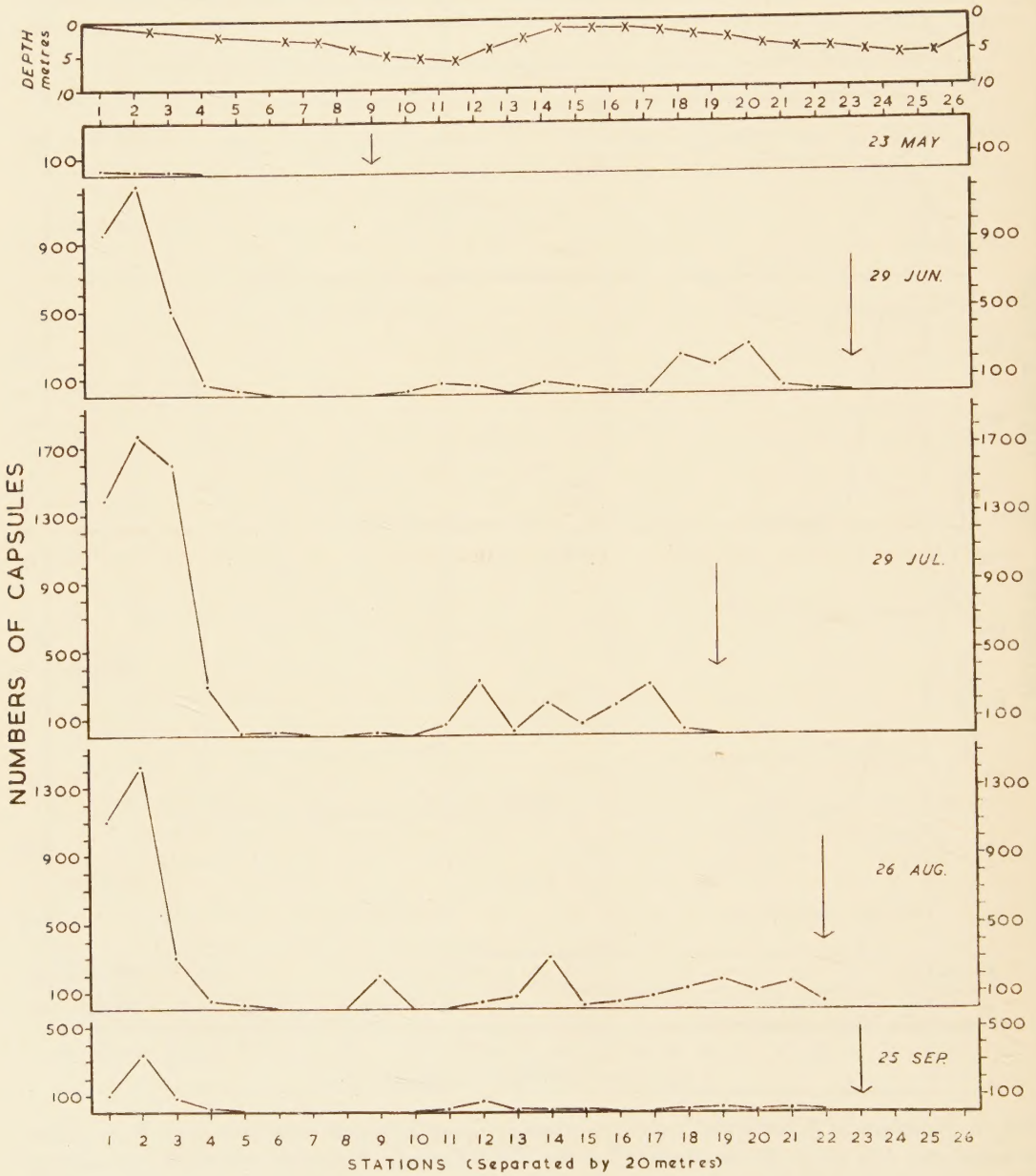


Fig. 5. *Numbers of* Urosalpinx *capsules taken in standard parallel hauls with two* 4 *ft.* 6 *in. power dredges over* 125 *m. at the Southward Laying, River Crouch, in* 1955, *commencing* 10 *m. from L.W.O.S.T. on the north shore. A section across the river showing mean depths is given. The final dredge station on each date is indicated by an arrow.*

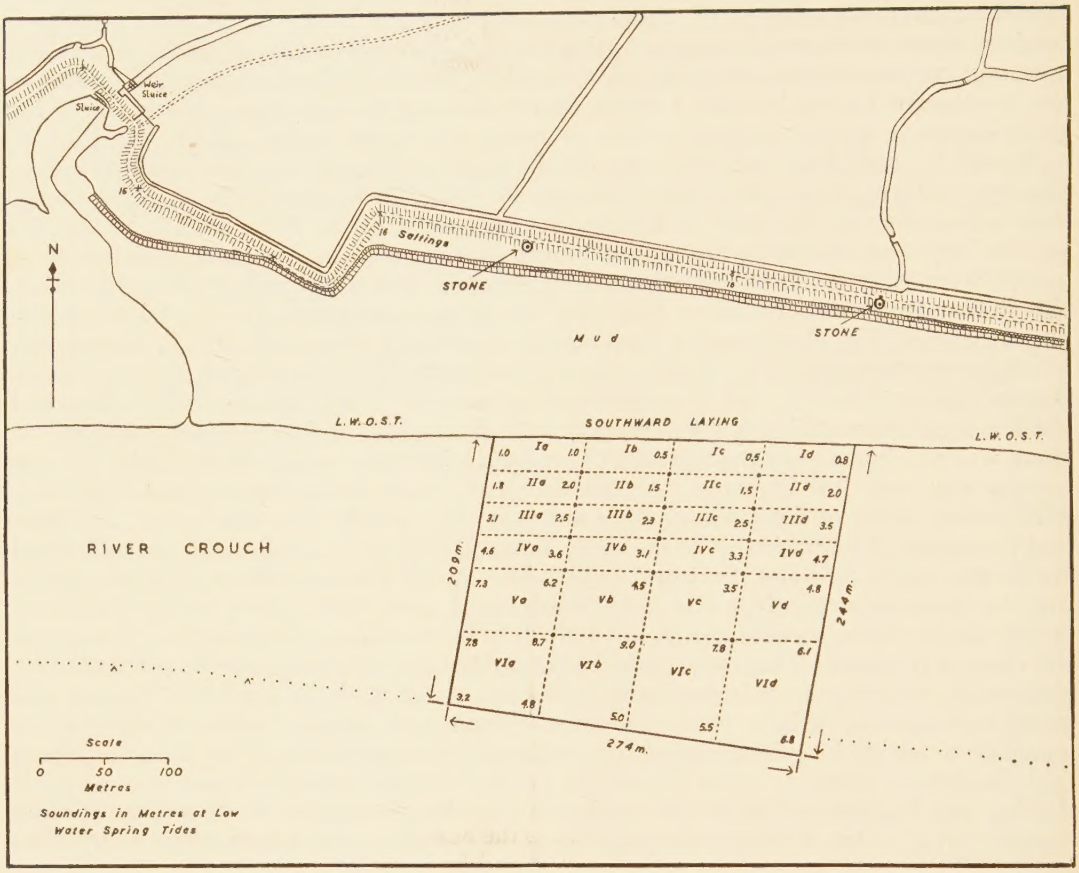
grab survey (Stations c, d, and continuing offshore (Fig. 6)). Results (Figs. 4 and 5) showed that the main concentrations of tingles occurred between L.W.O.S.T. and 60 m. offshore. Again numbers increased during the spring because of increased activity by the tingles, and a certain amount of shoreward migration could be detected. Movement on to the shore at the Southward Laying is rather limited, despite the fact that the population is one of the most dense in the two rivers. A line of rocks, the 'stone hedge', marks the limit of L.W.O.S.T., and these and tile traps on the shore, examined regularly, yielded only a fraction of the numbers taken above low-water-mark at the Common Shore. A few tingles were again taken on the shore in January but only up to about 10 m. from L.W.O.S.T.; mostly they were buried in the mud or under shells and rocks. Relatively few tingles or spawn were taken offshore, and these were generally associated with a submerged bank 240–400 m. from the north shore. Dredging was seldom extended to the south shore which shelves steeply (Fig. 4) with only a short stretch of soft mud above L.W.O.S.T. The scarcity of tingles on Stations 6–11 is not believed to be the result of increased depth, since maximum depths were only 6–7 m., and *Urosalpinx* and spawn were found offshore in both deep and shallow areas; more probably it was related to the distribution of food. Around Stations 6–11 there was an almost pure population of *Crepidula* with many empty shells (Table 15), no oysters and very few barnacles. At the Common Shore laying too, oysters were only occasionally found offshore among large numbers of *Crepidula*. Distribution of *Urosalpinx* and the extent of migration on to the shore above L.W.O.S.T. is believed to be influenced by the amount of food and the degree of exposure. At the Common Shore, food is plentiful and the shore slopes gently, while at the Southward Laying there is little food on the shore, which slopes rather more steeply. Below L.W.O.S.T. the main concentrations of *Urosalpinx* are close to the shore. This seems to be its natural habitat, but it is probably influenced by cultivation, whereby areas immediately below low-water-mark are cleaned of limpets and relaid with oysters, while in many places the offshore parts remain derelict. A study of the population density by grab sampling has confirmed this distribution at the Common Shore and Southward Laying, while Mistakidis (1951) obtained similar results on the Shop Laying and Paglesham Reach. He concluded that the distribution of *Urosalpinx* showed clearly that it prefers a bottom carrying a good deal of shell or in a fair state of cultivation.

III. POPULATION DENSITY

Several authors in America have counted the numbers of tingles on exposed intertidal areas and obtained figures varying from 29 per sq. m. on flat intertidal bottom to 947 per sq. m. on an intertidal oyster reef (T. C. Nelson, 1922 and Stauber, 1943 *cit.* Carriker, 1955). In this country, Mistakidis (1951) used a Petersen grab and found up to 6 tingles per sq. m. on the Southward Laying and up to 5 per sq. m. in Paglesham Reach. He concluded that the distribution of tingles on oyster layings is correlated with the presence of patches of firm shelly ground, and that they do not occur in any quantity on pure mud. A knowledge of the numbers of *Urosalpinx* on an area of oyster bottom is of great importance when assessing the amount of damage they may cause, the efficiency of gear and the effectiveness of control measures.

1. GRAB SURVEYS

The method used by Mistakidis (1951) has been followed, and can be expected to give a reasonable guide to the distribution of *Urosalpinx*. In August–September, 1952, a survey was made at the Southward Laying, but using a 1/10th sq. m. van Veen grab instead of the Petersen grab used by Mistakidis; the former is generally more efficient (Thamdrup,



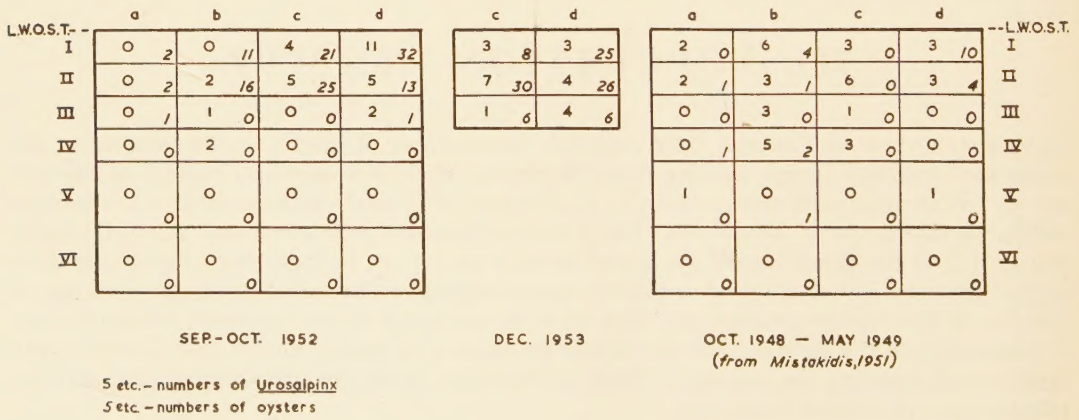


Fig. 6. *Map showing the Southward Laying, River Crouch, with the position of grab survey stations, and approximate depth in metres (after Mistakidis,* 1951). *The numbers of* Urosalpinx *and oysters per square metre from* 10 *grab hauls on each station are shown diagrammatically below.*

Table 1: *Density per sq. m. of* Urosalpinx *and other species on the Southward Laying, River Crouch, from* 10 *grab hauls taken at each station between* 28 *August–*23 *September*, 1952

Station	Urosalpinx		*Oysters*	Crepidula *chains*	*Nature of Bottom*
	Live	*Dead shells*			
Ia	–	–	2	–	Soft black mud; little shell.
IIa	–	4	2	–	Soft black mud; little shell.
Ib	–	–	11	–	Shell and mud.
IIb	2	–	16	–	Shell, shell gravel and mud.
Ic	4	2	21	–	Shell, shell gravel and mud.
IIc	5	2	25	–	Much shell and brown mud; *Buccinum.*
Id	11	3	32	–	Shell and mud; *Buccinum.*
IId	5	–	13	–	Shell, shell gravel and mud.
IIIa	–	–	1	few	Mud; little shell.
IVa	–	–	–	13	Mud; little shell.
IIIb	1	–	–	few	Mud; little shell; *Buccinum.*
IVb	2	–	–	45	Mud; some shell; *Buccinum.*
IIIc	–	–	–	–	Mud; some shell and shell gravel.
IVc	–	–	–	51	Mud and shell; *Buccinum.*
IIId	2	–	1	few	Mud and shell; *Asterias.*
IVd	–	1	–	many	Mud; some shell.
Va	–	–	–	85	Mud; little shell.
VIa	–	–	2	27	Mud and shell; *Buccinum.*
Vb	–	–	–	219	Mud and little shell.
VIb	–	–	–	25	Mud and little shell.
Vc	–	–	–	106	Mud and some shell.
VIc	–	–	–	82	Shell, shell gravel and mud.
Vd	–	–	–	131	Some shell, stones and mud.
VId	–	–	–	48	Mud, gravel and little shell.

1938). In these surveys the standard van Veen sampler was found to behave more effectively when four 9 lb. lead slabs were bolted to the outside of the buckets, two on each side. The oyster laying was divided up by beacons and buoys and ten grab hauls were made at random in each area. The results are compared with those of Mistakidis in Fig. 6. Densities are of the same order as found in 1948–49, but it appears that a regrouping of the population has occurred, and the maximum density, 11 per sq. m., was found associated with the largest number of oysters. A similar survey over only part of the area in December, 1953 (Fig. 6), showed a distribution more like that found by Mistakidis, whose survey of this part of the area in October–November, 1948 was made at a comparable time of the year. It is believed that the concentrations were largest nearer the shore in 1952 because of the shoreward migration which had occurred during the summer. More evidence of this movement is presented below (see p. 13), and these results may be compared with those of dredge surveys made on the Southward Laying (Fig. 4). The absence of tingles from Stations (I–V)a, was associated with a high proportion of black mud with only a little shell and few oysters. On Stations V–VI the fauna was composed almost exclusively of *Crepidula* (Table 1). It is interesting to compare the figures for *Crepidula* individuals obtained by Mistakidis (1951) with those of *Crepidula* chains taken in this survey (Table 1). The great reduction in numbers on Stations I–III is the result of cultivation of the bottom (including removal of *Crepidula*) followed by relaying of oysters.

A similar survey was made at the Common Shore, River Roach from the 17th–21st August, 1953. The results are given in Fig. 7 and Table 2. A maximum of 6 tingles per sq. m. was found at 20–40 m. below L.W.O.S.T. This compares well with the results of the dredge survey of this ground made in the same year (Fig. 3). It must be remembered that a proportion of this population was on the shore as a result of the summer migration. From this survey, it was estimated that there were some 32,000 tingles on the Common Shore oyster laying.

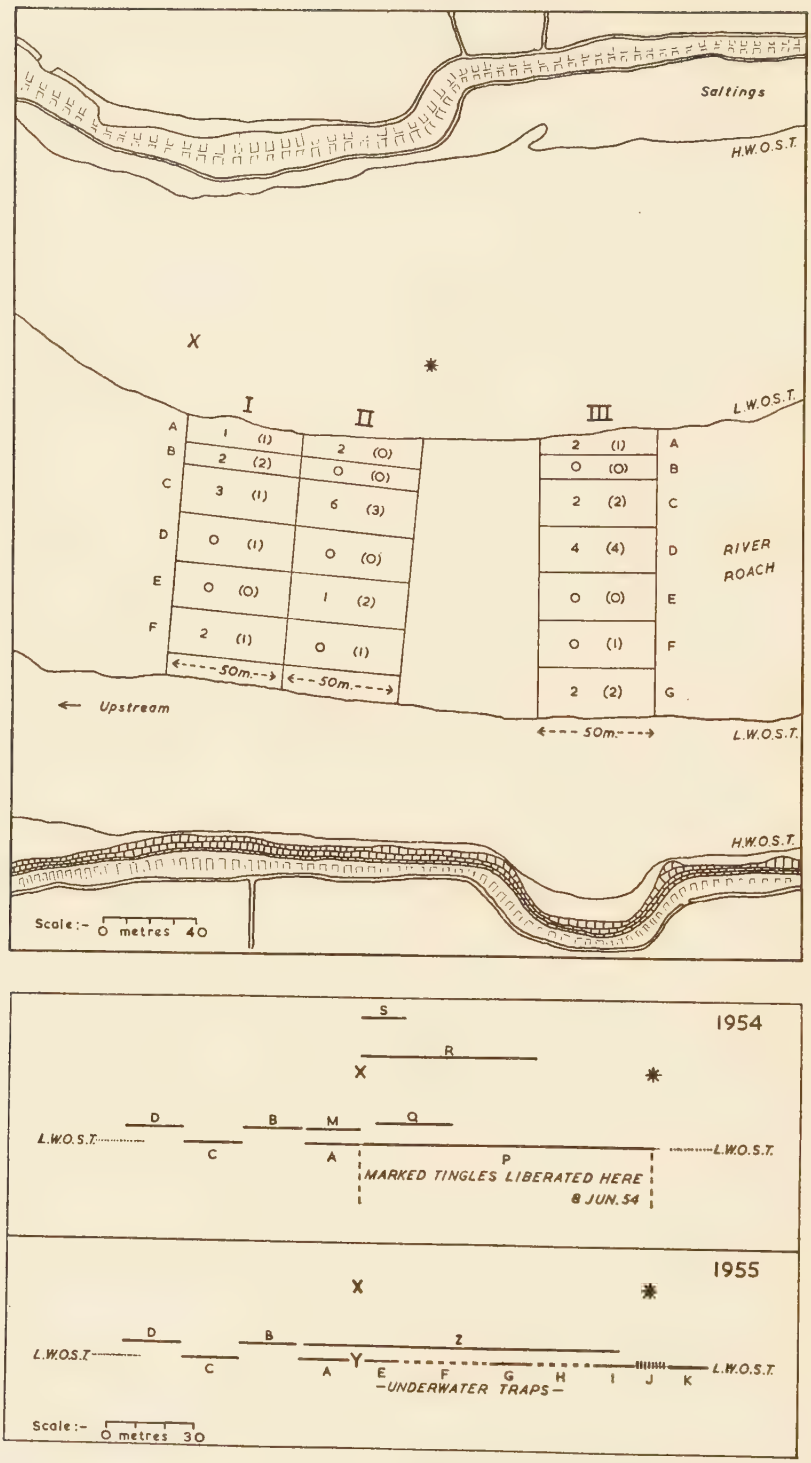


Fig. 7. *Map showing the Common Shore, River Roach, with the position of the grab survey stations. The numbers of* Urosalpinx *per square metre from* 10 *grab hauls on each station are shown, with (in brackets) the numbers of oysters. The arrangement of rows of tile traps at and above L.W.O.S.T. in* 1954 *and* 1955 *is shown diagrammatically below (* marks the position of liberation of marked tingles on* 22 *August,* 1952—*see also Fig.* 8, *X and Y positions of liberation of marked tingles on* 7 *June,* 1955).

Table 2: *Density per sq. m. of* Urosalpinx *and other species on the Common Shore, River Roach, from* 10 *grab hauls taken at each station between* 17–21 *August*, 1953

Station	Urosalpinx		*Oysters*	Crepidula	*Others*	*Nature of Bottom*
	Live	*Dead shells*				
1A	–	1	–	–	12 *Cardium edule* 1 *Paphia aurea*	Mud, shell gravel, little shell.
1B	1	2	1	7 single	1 *C. edule* 4 *C. exiguum* 2 *Nassarius*	Mud, shell gravel, little shell.
1C	2	3	2	8 single	6 *Nassarius* 2 *Cliona*	Mud, shell gravel, shell.
1D	3	–	1	3 chains 2 single		Mud, shell gravel, shell.
1E	–	2	1	6 chains 14 single	1 *Nassarius* 1 *Paphia aurea* 1 *Mya*	Mud, shell gravel, little shell.
1F	–	–	–	5 single		Mud, little shell gravel.
1G	2	–	1	5 chains	1 *Nassarius*	Mud.
2B	2	1	–	5 chains 12 single	2 *C. edule* 1 *C. exiguum* 1 *Buccinum*	Mud, shell gravel, small shell.
2C	–	1	–	10 single	2 *C. edule* 2 *C. exiguum* 1 *Nassarius*	Mud, shell gravel, small shell.
2D	6	5	3	6 chains 63 single	8 *Nassarius* 3 *C. exiguum*	Mud, shell gravel, small shell.
2E	–	2	–	2 chains	2 *Nassarius*	Mud, very little shell.
2F	1	–	2	2 chains	2 *Nassarius*	Soft mud, little shell.
2G	–	–	1	8 chains	2 *Nassarius* 2 *C. exiguum*	Mud.
3B	2	1	1	7 single	1 *C. edule* 1 *C. exiguum* 2 *Nassarius*	Mud, shell gravel, shell.
3C	–	–	–	–	1 *Paphia aurea* 1 *C. exiguum* 1 *Nassarius*	Mud, shell gravel, shell.
3D	2	3	2	28 chains 11 single	1 *C. edule* 1 *C. exiguum* 3 *Nassarius* 3 *Cliona*	Mud, shell gravel, little shell.
3E	4	–	4	19 chains 25 single	5 *Nassarius* 1 *Cliona*	Mud, little shell.
3F	–	–	–	–	1 *Nassarius* 1 *Cliona*	Mud, little shell.
3G	–	–	1	2 chains 1 single	1 *Nassarius*	Mud.
3H	2	–	2	13 chains	3 *Nassarius*	Mud.

2. MARKING EXPERIMENTS

The marking of animals for release and recapture often gives valuable information on their density and migrations. Tingles used in these marking experiments were cleaned and dried by exposure to the air for a few hours, and a coating of quick drying lacquer paint was applied to the spire with a brush. Shells dipped in paint became too thickly coated and took much longer to dry. Although cellulose paint dries very quickly, and is useful for immediate work such as determining population density by recapture, these studies were to be followed by long term observations on migration and for these, lacquer paint is better, showing less tendency to peel. Tingles thus marked have been recaptured more than two years after liberation with the paint easily visible. By using different colour combinations for each size-group, it was possible to measure the increments in growth between the times of marking and recapture.

Tingles collected on the previous day, marked, and allowed to recover overnight in a large tank of seawater, were scattered on 8th June, 1954, as evenly as possible from a small motor boat over an area 30 m. by 100 m. adjacent to L.W.O.S.T. at the Common Shore, i.e. in areas I and II A–B and half of C, used for the grab survey (Fig. 7). The tingles were left until the following day to allow mixing with the population (they have been found to attach quite quickly to the substratum when released). Eighteen parallel dredge hauls were made on the strip of experimental ground on the 9th June and the painted and unpainted tingles counted; 59 painted tingles were taken compared with 583 unpainted. Painted tingles were attached to shells indicating that they were behaving in no way differently from the unmarked population. The population on the marked area was calculated using Bailey's (1951) modification of the 'Lincoln Index'. This is: $\hat{x} = a(n + 1)/(r + 1)$ where $\hat{x}$ is the total population on the marked area, a is the number of individuals marked, and n is the total number in a random sample of which r are found to be marked.

$$\therefore \text{ Estimated total population} = \frac{577 \times 643}{60} = 6{,}184.$$

This, related to the area of 3,000 sq. m., gives a density of 2·1 tingles per sq. m. The average number per sq. m. calculated from figures obtained over the same area by grabbing was 2·3. The total number of tingles removed from the area by trapping and dredging between August, 1953 and June, 1954 was 1393, or 0·5 per sq. m., but, of course, replacement of part of the population by growth of some of the smaller tingles had also taken place. The results obtained by the two methods agree more closely than it is reasonable to expect, but it seems likely that they give a good picture of the numbers present. The surveys will be repeated, to help to estimate the effectiveness of control measures.

IV. MIGRATION

The migrations of *Urosalpinx* are of great importance in oyster culture, particularly when planning methods of capture and control. Federighi (1931) used several methods of marking *Urosalpinx*. In Hampton Roads, Virginia, he found that drills marked with pigment moved over oyster ground in deep water at a maximum rate of 10 ft. per day. At Beaufort, North Carolina, drills marked by a celluloid tag attached by fine silver wire to the outer lip of the shell moved over oyster beds, exposed or just below water at low tide, at only 0·4–0·5 ft. per day. This low rate may have been due to the impeding of movement by the marks. He concluded that extensive migration does not occur. The maximum rate of movement recorded in America was 75 ft. per day by Galtsoff *et al.* (1937) for tingles moving over a clean bottom to traps baited with oysters and placed from low-water-mark to 15 ft. below. They concluded that in the search for food *Urosalpinx* is able to travel a considerable distance, and that its places of concentration may be correlated with the presence of an abundant supply of oysters and other natural food. Carriker (1955), summarising the work

of several authors, concluded that the bulk of the drill population moves about to a rather limited degree, particularly over oyster bottom. Previous workers in this country (Orton 1930, Cole 1942, Mistakidis 1951) have suggested that an inshore spawning migration takes place but there has been little substantiating evidence.

Tingles marked for population density studies on the 8th June, 1954 appeared later among those taken in regular collections from tile traps (see p. 54) in 1954 and 1955. The 577 tingles marked had been obtained from the shore at L.W.O.S.T. (Row P – Fig. 7) and were distributed among the population between L.W.O.S.T. and 30 m. offshore. The numbers of tingles retaken, their date of recapture and the index of the row of tile traps are shown in Table 3 which should be used with reference to Fig. 7. 281 tingles have so far

Table 3: *Recovery of marked tingles from tile traps on the Common Shore, River Roach, in* 1954–1956. *Tiles were rearranged after 7 May*, 1955 (*see Fig.* 7)

Date	*Row*								
	D	*C*	*B*	*A*	*P*	*M*	*Q*	*R*	*S*
2 Jul. 54	–	–	–	–	1	–	1	–	–
19 Jul. 54	–	–		2	11	–	–	1	–
3 Aug. 54	–	–	–	–	6	2	–	–	–
17 Aug. 54	–	–		1	10		4	1	–
31 Aug. 54	–	–	–	1	7	–	–	–	–
15 Sep. 54	–	–	–	1	7	–	–	–	–
29 Sep. 54	–	–	–	1	5	1	–		–
15 Oct. 54	–	–	–	–	8	1	1	–	–
1 Nov. 54	–	–	–	–	4	1	1	–	–
15 Nov. 54	–	–	–	2	3	1	–	–	–
26 Apr. 55	–	–	–	1	5	–	–	–	–
7 May 55	–	–	1	2	14	1	4	–	–
TOTAL	–	–	1	11	81	7	11	2	–

Date	*Row*												*Trap Line*
	D	*C*	*B*	*A*	*E*	*F*	*G*	*H*	*I*	*J*	*K*	*Z*	
24 May 55	–	–	–	–	2	4	1	–	–	–	–	1	–
7 Jun. 55	–	–	–	–	–	–	–	–	–	–	–	3	–
22 Jun. 55	–	–	–	1	6	24	7	4	–	–	1	3	26
7 Jul. 55	–	–	2	1	8	–	2	3	–	2	1	5	15
22 Jul. 55	–	–	–	–	1	5	–	–	1	–	–	–	6
5 Aug. 55	–	–	–	–	–	3	1	1	–	–	–	2	1
19 Aug. 55	–	–	–	1	–	–	–	–	–	–	–	1	–
5 Sep. 55	–	–	–	–	–	1	–	–	–	–	–	1	2
20 Sep. 55	–	1	–	–	–	–	–	–	–	–	–	–	–
5 Oct. 55	–	–	–	–	–	–	–	1	–	–	–	–	1
14 May 56	–	–	–	1	–	1	–	1	–	1	–	–	4
26 May 56	–	–	–	–	1	1	–	1	–	–	–	–	–
11 Jun. 56	–	–	–	–	–	–	1	–	–	1		–	–
10 Jul. 56	–	–	–	1	–	–	–	–	–	–	–	–	1
8 Aug. 56	–	–	–	–	–	–	–	–	–	–	–	–	1
TOTAL	–	1	2	5	18	39	12	11	1	4	2	16	57

been recaptured representing nearly 50 per cent of those marked; others will no doubt be taken later. From this experiment it can be seen that a large proportion of the tingles moved at some time on to the shore, the greatest distance recorded above L.W.O.S.T. being 30 m. on Row R. A limited number moved upstream on to Rows A–C, the farthest distance travelled being about 50 m. In 1956, six were taken from underwater traps just outside the eastern edge of the marked area; one was 50 m. away. These figures represent the minimum distance moved by each tingle, since marked tingles may have originated from any position in the area of 30 by 100 m., and did not necessarily move in a straight line. The results are sufficient to show that some, at least, of the tingles taken high up on the

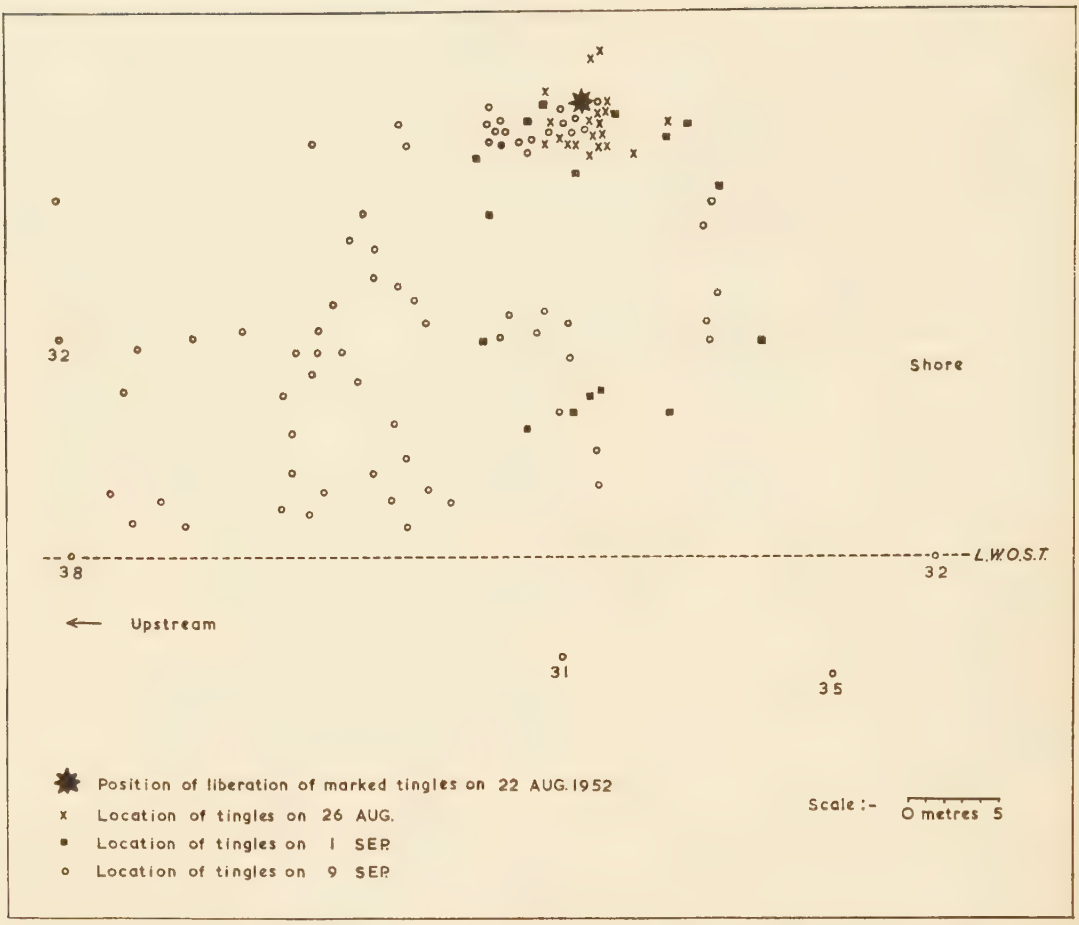


Fig. 8. *The progressive movement of* Urosalpinx *from a group of* 500 *marked individuals placed* 25 *m. above L.W.O.S.T. on the Common Shore, River Roach, on* 22 *August*, 1952. *Numbers show the maximum recorded distances in metres individual tingles travelled by* 9 *September*, 1952.

shore had come from below L.W.O.S.T., and that a certain amount of horizontal migration also took place.

Other experiments included the marking of groups of tingles and their subsequent observation on the shore. On the 22nd August, 1952, 500 marked tingles taken from tiles at L.W.O.S.T. (Row P, Fig. 7) were placed 25 m. above L.W.O.S.T., the spot being marked by a beacon. Fig. 8 shows the position of all tingles recovered on subsequent inspection dates. On the 26th August, after $3\frac{1}{2}$ days, the greatest distance moved was 5 m., equal to 1·4 m. per day; on 1st September, 18 m. or 1·9 m. per day and on 9th September, 38 m. or 2·2 m. per day. Although movement has been expressed as metres per day, the tingles were uncovered by the tide for periods of up to an hour or so around low water. At the end of the period of observation some tingles had obviously moved below L.W.O.S.T. The shore over which the tingles moved was of fairly firm mud, with small shell and clumps of larger shells, mussels, *Littorina* and some oysters. There were patches of softer mud with no shells which seemed to slow down movement but not to stop it completely. The general movement was downshore and upstream. Larger areas of soft mud to the downstream side of the beacon may have been the cause of the smaller number of tingles taken there. Virtually no upshore migration took place. On the 20th September, 1952 only 30 tingles were still to be found very close to the beacon. On the 21st October, several were found on tiles up to 60 m. from the point of liberation. In the following year 20 tingles were still close to the beacon on the 8th May, 1953. On the 1st October, 1953 two were dredged up

15 m. below L.W.O.S.T., on 13th November, 1953 one from 35 m., and on 9th June, 1954, one from 15 m. and another from 30 m. below L.W.O.S.T. On the 4th June and 2nd July, 1954 respectively, two tingles were taken on Row A (Fig. 7) representing a migration of at least 110 m. from the beacon.

On the 7th June, 1955, 265 marked specimens of *Urosalpinx* were liberated at L.W.O.S.T. (position Y on Fig. 7) and 265 with different markings at a point 25 m. upshore (position X on Fig. 7). Here the bottom was fairly even and composed of firm mud with shell gravel, shells, oysters and mussels. Those liberated at the upshore position X moved down towards L.W.O.S.T. in general, showing both upstream and downstream movement. Those released at L.W.O.S.T. (position Y) showed some movement upshore up to 10 m. above L.W.O.S.T., but generally the movement was upstream and downstream. The positions of nearly 50% of each group were plotted on the 22nd July, showing that, allowing for the large number which must have been overlooked because of silting, a very high proportion remained on the shore for some time. Tingles from position X had then moved up to 60 m. from their original position, and from position Y, a maximum of 82 m. This represents a movement of 1·8 m. per day, closely agreeing with previous observations. By the 18th November, only 29 from the upper beacon and 8 from the lower beacon were visible and it was concluded that the remainder had moved below L.W.O.S.T.

Evidently, *Urosalpinx* can move about at a rate of approximately two metres per day, and at this rate could travel quite a considerable distance in one season. The main part of the movement is probably associated with spawning, but there is also a certain amount of horizontal migration. In general, tingles released at L.W.O.S.T. showed a marked upshore migration, while those released 25 m. upshore moved down the shore to below L.W.O.S.T., directly in winter, but seeming to find a level of about 5 m. above L.W.O.S.T. satisfactory in summer. Some tingles are taken on the shore even in winter but they are usually buried under rocks and shells.

Evidence of the movements of *Urosalpinx* below low-water-mark has been obtained from the dredge surveys outlined in the previous section. On the Common Shore, there is a marked movement to the shore during the summer, which is evident from the catches taken in parallel dredge hauls. In Fig. 3 it can be seen that the largest numbers were dredged from May to June, 1953. On the 18th May peak numbers were caught at Stations 1 and 3; by the 3rd June the peak on Station 1 was no longer present, and on 19th June there was one large peak at Station 2. The peak in dredged catches on the 19th June was not evident in subsequent dredging, but preceded the largest catch of the year of tingles and spawn on shore traps; this occurred on the 1st July. The amount of spawn deposited on inshore stations also increased about this time. The sudden increase in numbers in the dredged catches after the 8th May can be explained as due to increasing activity as the temperature rose. On the 18th May the inshore stations showed a higher proportion of males, and it appears that this resulted from a greater initial activity by the males. This was not evident in catches on tiles at Common Shore as these always yield a higher proportion of females (Table 8) since the tiles are selected as a spawning, rather than a feeding, site. On the Southward Laying, however, it is found that in April, after hibernation, there is a much greater preponderance of males showing activity than later in the season. On the Southward Laying less migration takes place on to the shore. Fig. 4 however shows the great increase in the numbers of tingles dredged from June–August as a result of increased activity and throughout these months there is a tendency towards increased density on the stations nearest L.W.O.S.T. A trapping experiment by G. D. Waugh (personal communication) at the Common Shore has been described in a later section (p. 41) and his results analysed in Fig. 20. These show a definite and sustained increase in the numbers of tingles and spawn taken on inshore stations in June and July, 1950, as a result of the onshore migration.

An examination of the quantities of tingles and spawn taken on rows of tile traps (Fig. 24) shows that large numbers of tingles and spawn were found on Rows A and C on the 21st May, 1954, but not until 3rd June on Rows B and D. The shapes of the graphs indicate a wave of onshore movement of tingles, which is further borne out by studying Row M, on which the numbers taken reveal the screening influence of Row A farther down the shore. The positions of the rows of tiles are shown in Fig. 7.

It may reasonably be concluded that there is a substantial movement of tingles to the shore during the spawning season, some moving up to at least 45 m. above L.W.O.S.T. Although the largest proportion of the total spawn is found below L.W.O.S.T., this too seems to be deposited during the shoreward migration. These observations are of great importance when planning methods of control by trapping and dredging. The factors producing this movement are not very clear. In general the onshore migration is not from a region of little to more food, since at the Common Shore, although there is plentiful food on the shore, it is even more abundant below L.W.O.S.T. At the Southward Laying, however, there is very little food on the shore, and also very little migration above L.W.O.S.T. It is considered that this movement is more likely to be due to a negative geotropic response, and is perhaps limited by degree of exposure.

V. FEEDING

Urosalpinx feeds by attacking other shellfish, and uses its radula to drill a neat circular hole through the shell of its prey. The proboscis is inserted through the hole, and the flesh of the prey is rasped away by the radula and devoured. Carriker (1943) described the structure and functions of the organs concerned in the drilling mechanism, and suggested that drilling appears to be aided by the softening action of secretions from what he called the accessory proboscis, located in the foot.

Previous work has established without doubt that *Urosalpinx* feeds extensively on oysters, and particularly oyster spat. Carriker (1955) has given a comprehensive account of observations by many authors on its food and feeding behaviour in the United States.

1. TEMPERATURE AND FEEDING

In the United States the temperature at which drilling commences varies in different localities (Carriker, 1955), from 6·5°C. in Virginia (Andrews and McHugh, *cit.* Carriker, 1955) to 15°C. in North Carolina and Virginia (Federighi, 1931). Cole (1942) found that in England drilling commenced as soon as the water temperature exceeded 11–12°C., usually in April or early May, but little feeding occurred then as the drills were actively spawning. In June, when the peak of spawning had passed, intensive feeding began and continued until the water temperature again dropped below 11–12°C., usually at the end of October.

Urosalpinx kept in the laboratory in 1953 continued feeding until the middle of December when the average water temperature dropped to 9–10°C. (Fig. 9). In a second smaller tank, temperatures remained above 9–10°C. for a longer period and on the 23rd January, 1954 a tingle was still feeding at 9·5°C. The tingles gradually became quiescent as temperatures dropped to 5°C. and apart from some rare movements up the side of the tank, remained half-buried in the mud on the bottom, usually with only the tip of the siphon visible. As temperatures rose above 7°C. (Fig. 9), progressively more movement occurred and on the 10th March, with the temperature at 9°C., many tingles had moved up the sides of the tank. On the following day, one spat was drilled as the temperature rose to 10·5°C., and two other tingles commenced feeding before the temperature began to fall on the 13th March. By the 16th March the temperature had fallen to 7·5°C., feeding had ceased and half the tingles had returned to a hibernating condition on the bottom. A rise in temperature to 8–9°C. on the 20th March brought a great increase in activity, and feeding recommenced on 21st March at a temperature of 9–10°C. A small proportion of the tingles remained buried for several weeks even when the temperature reached 11°C., but all had left the bottom by the 30th April when the first capsule was laid at a temperature of 11·2°C. The temperature had not previously risen above this level. Although some feeding had taken place the majority of tingles were congregated in one position on the side of the tank,

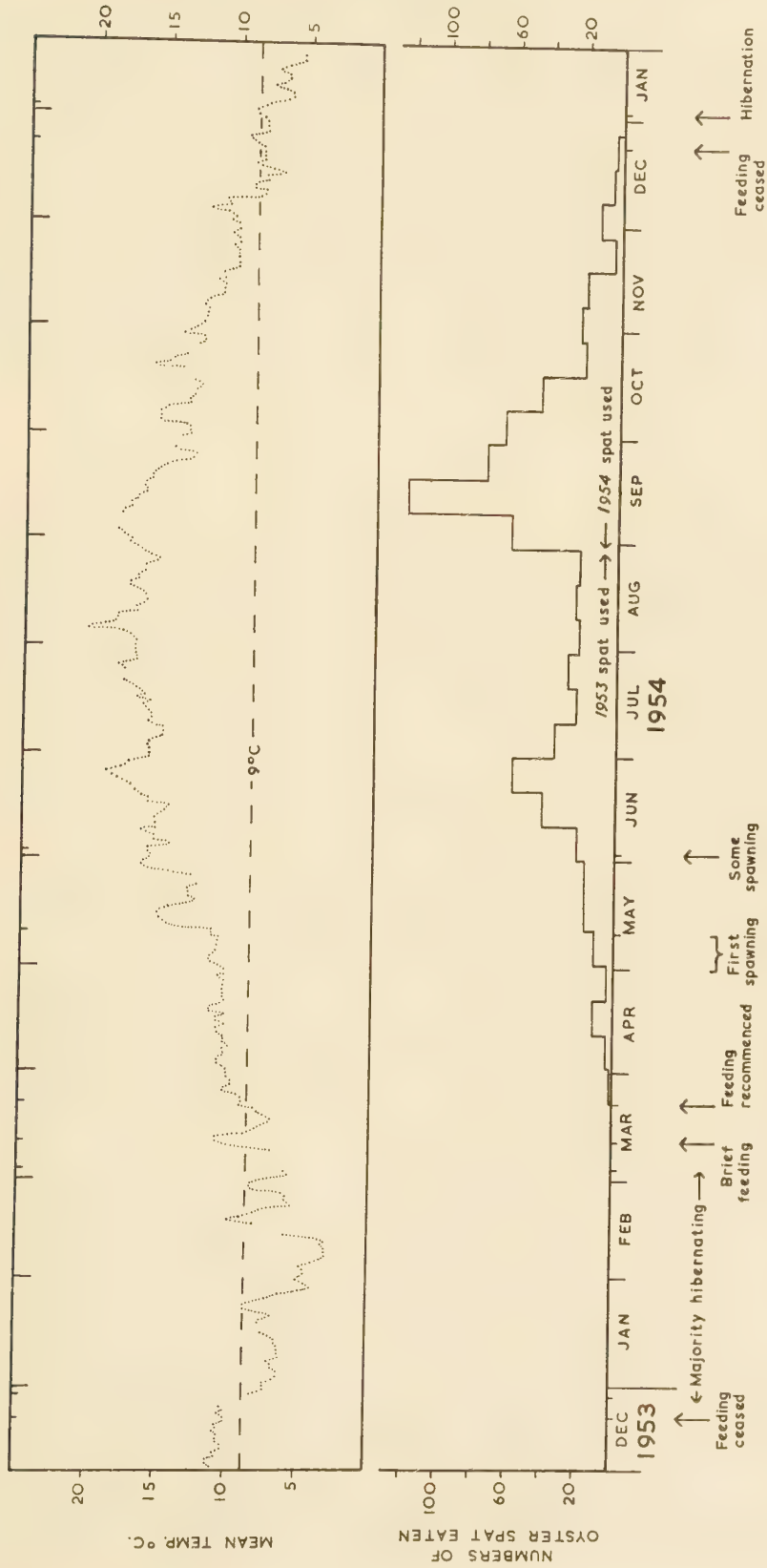


Fig. 9. *Numbers of oyster spat eaten in* 10*-day periods by* 20 Urosalpinx *in the laboratory in* 1953–54. *Mean daily water temperatures in* °*C. recorded during the experiment are given.*

and on examination it was seen that this was the place at which the inflow stream of water was directed against the side, the tingles having exhibited a negative rheotaxis.

In a parallel experiment, commenced on the 22nd March, 1954, 20 adult *Urosalpinx* from Creeksea were confined with shells bearing 30 oyster spat and 30 *Crepidula* spat, each spat being replaced when eaten (Fig. 9). The mean temperature at the commencement of the experiment was 9·5°C. Only limited feeding took place before the 30th April when spawning commenced. Spawning continued until the 10th May, and was followed by more intensive feeding (Fig. 9). Females took part in the limited feeding which occurred before and during the spawning period. Feeding continued in this experiment until the 23rd December, 1954 when the mean temperature was 9°C. It appears from these observations that 9–10°C. is the usual lower limit for feeding, at least in the laboratory. Temperatures above 9–10°C. are usually reached in the rivers in April and persist till the end of October. At the beginning and end of the feeding period there are more oysters on which drilling or feeding has not been completed.

2. RATE OF FEEDING

Carriker (1955) has summarised the feeding rate observed by different authors for *Urosalpinx* from different localities. It appears that the rate of feeding increases proportionately with both the size of the tingle and the water temperature. Cole (1942) correlated the daily rate of destruction of oyster spat and water temperature. He concluded that adult tingles fed on one-year-old spat at a rate of 0·332–0·481 spat per tingle per day, and on two-year-old brood oysters at 0·034 oyster per tingle per day. Fig. 9 also demonstrates the relationship between feeding rate and temperature. Increases in feeding rate, for example, during June and also the commencement of feeding, seem to occur after a sustained rise in temperature. In the feeding experiments described earlier, oyster spat which had settled in the previous year, 1953, were used until the end of August, when they became less easy to obtain. Smaller spat of about 5 mm. diameter, which had settled in 1954, were then used. Over the whole period of the experiment, therefore, the age of the spat used varied from a few weeks to one-year-old. Fig. 9 shows the total numbers of oyster and *Crepidula* spat eaten in periods of 10 days by 20 *Urosalpinx*. Over the period of 286 days a total of 752 oyster spat and 64 *Crepidula* spat were eaten, representing an average of 0·143 spat per tingle per day, and including a maximum of 0·630 per day and a minimum of 0·005 per day. The average number of spat eaten per tingle between the end of July and early November was 23, and included 2·3 large spat (settled in 1953) and 2·5 *Crepidula* spat. This figure agreed well with the estimate of 20 spat per tingle eaten at the Southward Laying over a similar period in 1953 (Hancock, 1954). On the basis of these results from the field and laboratory, it is estimated that each tingle is capable of consuming about 40 oysters of 5–20 mm. average diameter in Essex rivers each year, including oyster spat settled in both the same and the previous year.

In another experiment made in September 1954, one tingle consumed seven 5 mm. spat in 7 days at temperatures of 16·5 to 18·3°C. Newly-hatched tingles have been shown to be capable of feeding on oyster spat or barnacles (Cole, 1942 and Hancock, 1954). Cole (1942) observed that juvenile tingles could eat 1·39 newly settled spat in 24 hours. Small tingles are able to attack brood oysters. Two 18 mm. tingles were observed attacking and devouring a 40 mm. oyster, and a 14 mm. tingle devoured a 38 mm. oyster.

Orton (1927) found that an adult *Urosalpinx* takes 5–6 days to attack and devour a brood oyster. Cole (1942) found at Conway that the average rate of destruction of brood oysters was one in 33 days. Carriker (1943) stated that perforation takes from two to seven days on oysters from $1\frac{1}{2}$ to 4 inches in diameter respectively. A short experiment in 1953 showed that in the presence of barnacles and other encrusting organisms, 20 tingles devoured 6 brood oysters in 26 days at 17–19°C. Only 6 of the tingles attacked the oysters, giving a feeding rate of 0·038 oyster per tingle per day, which closely agrees with Cole's (1942) figure of 0·033 per day in 1940 and 1941. In one experiment an adult tingle took $27\frac{1}{2}$ hours at

20°C. to drill through the shell before devouring a young 18 mm. *Crepidula*, suggesting that *Urosalpinx* encounters more difficulty in drilling the shell of a slipper limpet than that of an oyster spat of a similar size.

3. FEEDING BEHAVIOUR

Carriker (1943) has given a full account of his observations on drilling and feeding. When the tingle has chosen its drilling point, it alternately rasps with its radula and 'softens' by the accessory proboscis until penetration is completed.

During drilling the spire is sometimes seen to move in an anti-clockwise direction for at least 360°. This procedure has also been observed in *Ocenebra*. Oysters drilled at Creeksea, River Crouch, in 1953 were examined for the distribution of the perforations, which is

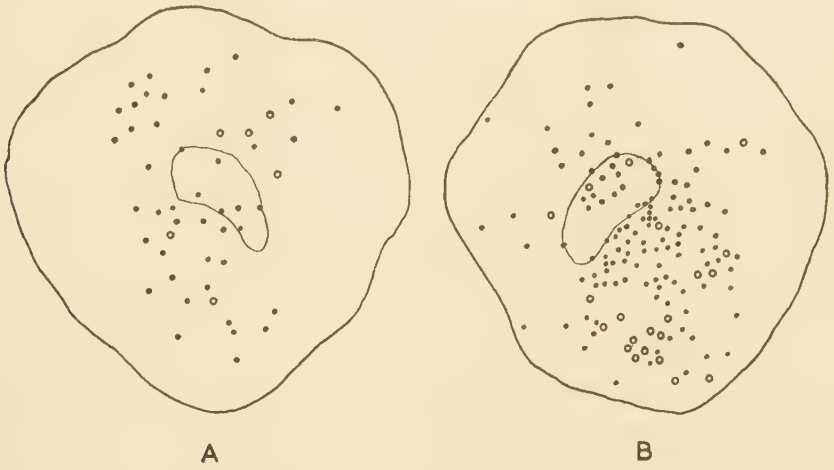


Fig. 10. *Inner surfaces of* (A) *the cupped valve and* (B) *the flat valve of a pair of oyster shells, showing the collected records of complete* (●) *and partial* (○) *drill holes in* 178 *paired shells from oysters drilled at Creeksea,* 1953.

shown in Fig. 10. 133 oysters had been drilled through the flat valve, and 45 through the rounded valve. This agrees with the work of various American writers (*cit.* Carriker, 1955), who, however, suggested that the flat valve is usually perforated since it is generally uppermost. On well-stocked beds in this country, observations have shown that the rounded valves of oysters are usually uppermost, suggesting that the oysters are most often drilled from underneath. There were 21 incomplete perforations on the flat valves and 6 on rounded valves. There were several instances of freshly drilled oyster shells showing, in addition to normal drill holes, perforation from the inside through to the outside. Further anomalous behaviour is sometimes exhibited when drills bore into oyster spat through the thick oyster shell on which they were settled. Drill holes are frequently found through the thickest part of the shell. In fact, the region most usually drilled, that is between hinge and muscle, is by no means the thinnest part of the oyster shell. Tanaka (1948–9) found that *Purpura clavigera* always drilled the right valve, usually at the shell margin. Orton (1927) stated that oysters are frequently attacked and abandoned when partly bored, or when a chamber or loose horny layer is encountered. In a sample from Creeksea, of 131 pairs of drilled oyster shells, 4 were perforated except for an inner covering of horny material, and 3 were completely drilled through additional horny material. The occurrence of a layer of horny material, probably conchyolin, covering a drill hole on the inside of a live oyster is not infrequent. It is believed to be deposited by the oyster as a means of closing the hole when the tingle has ceased drilling through disturbance or fall in temperature. An oyster from

the Helford river had been drilled in three places by *Ocenebra* but each drill hole had been closed in this way. The deposition of a horny protective layer by the oyster has been demonstrated in attacks by *Odostomia* (Cole and Hancock, 1955), and it may be that at low temperatures, when the rate of drilling by tingles is slow, the oyster can in this way offer some resistance to attack. The oyster illustrated in Fig. 11 was eventually killed after drilling by

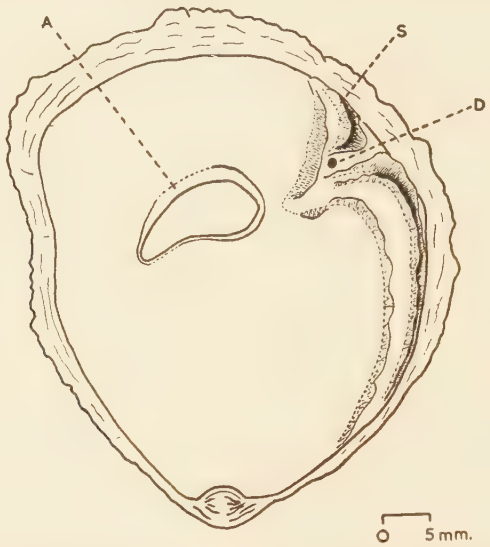


Fig. 11. *Inner surface of the flat shell of an oyster showing* (D) *the hole drilled by* Urosalpinx, (S) *deposits of shell material produced round it by the oyster and* (A) *the adductor muscle.*

Urosalpinx in the laboratory in April, 1954 when, at temperatures of 10–11°C., drilling was very slow and perhaps intermittent. The distribution of the horny deposition is typical of this condition and leaves little doubt that it was not encountered fortuitously, but was deposited in response to drilling. To find how quickly an oyster can close off perforations in its shell at these temperatures, holes similar to those bored by *Urosalpinx* were made in a series of oysters with a hand drill. In February, 1956, holes near the edges of oysters had been covered over in 9 days at a temperature range of about 7–11°C. Holes drilled between the adductor muscle and the hinge were not covered after 15 days when the experiment was ended. In October–November, 1956, the holes drilled in two oysters near the edge of the cupped valve were covered after 14 days at a temperature of about 8–11°C. Of two oysters drilled in the middle of the flat valve, one had commenced covering the hole after the same period, but the other showed no response, even after 26 days. Of two oysters drilled in the middle of the cupped valve, one had begun covering the hole after 26 days, the other not at all.

4. RECORDED DAMAGE TO OYSTERS

It was shown (Hancock, 1954) that 73% of oyster spat of 4–5 mm. and larger, which had settled on the Southward Laying in the summer of 1953, were dead by December; 58% of the spat had been destroyed by *Urosalpinx*. The figure represented the mortality of only half the year and did not include spat smaller than 4–5 mm. which fall ready prey to newly-hatched tingles. It was not difficult therefore to agree with Cole's (1951) estimate that 75% of oyster spat in Essex rivers are destroyed during their first year of life by *Urosalpinx*. Over an area of 6,250 sq. m. (Stations Ic–IIc and Id–IId, Fig. 6) at the Southward Laying, a grab survey showed that 86 spat per sq. m. had been destroyed. On the laying at Creeksea, 55% of the easily visible spat were destroyed in the same period. Orton (1937) estimated

that 50% of a spatfall in the River Blackwater, Essex, were destroyed by *Urosalpinx*, but offered no supporting evidence. Using similar methods to those described (Hancock, 1954) it was shown that 49% of easily visible (4–5 mm. and larger) spat had been devoured in Thurslett Creek, River Blackwater, by the 19th September, 1955; *Urosalpinx* still had nearly two months to feed before winter hibernation. In North Channel, Tollesbury Fleet, 24% of the spat had been devoured by the same date. Again these figures did not include the high mortality among newly-settled spat. Undoubtedly, the most obvious damage caused by *Urosalpinx* is to oyster spat. Estimates of damage to older oysters show that, under certain circumstances, these also may be destroyed in large numbers. Usually the percentage of adult oysters destroyed is not large. In August, 1953, the following mortalities due to *Urosalpinx* were recorded at oyster grounds shown in Fig. 2:—

Broadrakes: Adults 0%, Brood 2·8%; Common Shore: Adults 0%, Brood 2·8%; Shop Laying: Adults 0·8%, Brood 0·7%; Paglesham Reach: Adults 0%, Brood 1·4%; Southward Laying: Adults 0%, Brood 0·8%; Creeksea: Adults 6·8%, Brood 10·2%.

These are minimum figures since they were estimated by examining only freshly-dead shells for drill holes and comparing their frequency with that of the live population. The division between brood and adult oysters was arbitrary, set at about 60 mm. average diameter. A high predation rate by *Urosalpinx* on oysters larger than spat is to some extent related to the abundance of the rest of the fauna. At Creeksea, where the highest figure was recorded, this may have been due to the small number of spat settling there in the previous two years, coupled with the fact that there is only a small natural barnacle population, on which tingles feed when spat is not readily obtainable. On the Southward Laying, barnacle settlement is much heavier than at Creeksea. In Paglesham Reach, the barnacle population is small but there are fewer tingles than on the other oyster grounds. From observations on previous spatfalls, the oysters at Creeksea were calculated to be at least three years old, and it was estimated that 25,000 brood and 1,200 adult oysters were devoured on this laying in the first half of the feeding period in 1953. The figures for the death rates of brood and adult oysters on other layings may not seem very high but, where oysters are laid in heavy concentrations on such highly cultivated grounds as the Southward Laying and the Shop Laying, it can represent a considerable loss. On stations I–IIc, and I–IId at the Southward Laying (Fig. 6) which cover 6,250 sq. m. of oyster bottom, it has been calculated from the results of the grab survey that a 1% mortality due to tingles would amount to the loss of about 1,500 oysters, and on the Shop Laying to about 2,500 oysters over the whole laying. At the Common Shore, the oyster population is small and a 1% mortality would represent only a few hundred oysters.

5. FOOD PREFERENCES

It has been observed that *Urosalpinx* in Britain will feed on a variety of molluscs including *Ostrea edulis* and its spat, *Mytilus edulis*, *Cardium* spp., *Paphia* spp., the American slipper limpet *Crepidula fornicata*, and barnacles *Balanus* spp. and *Elminius modestus* (Hancock, 1954). In the United States, it eats in addition soft and hard clams, scallops, small crabs, the carrion of fish and lower invertebrates such as encrusting bryozoans (Carriker, 1955). Observations there showed that certain animals, particularly *Anomia*, appear to possess a quality tending to repel oyster drills. Under some conditions cannibalism has been observed.

It was demonstrated (Hancock, 1954) that on the Essex oyster beds, *Urosalpinx* feeds preferentially on oyster spat. Although barnacles are eaten, tingles have been observed drilling young oysters, mussels and even *Crepidula* which were covered by live barnacles. Shells covered by live barnacles but bearing drilled oyster spat were frequently taken. Drilled shells of *Crepidula* spat were only rarely taken from oyster grounds, and only 3% of dead adult *Crepidula* shells were found to be drilled. Under some conditions in the United States, *Urosalpinx* was found to feed on *Mytilus* before attacking small oysters (Galtsoff *et al.*, 1937). Cole (1942), however, showed that tingles offered spat oysters and small mussels, destroyed practically all the spat before attacking the mussels. It is interesting to

compare this behaviour with that of *Ocenebra* and *Nucella*, both of which, particularly *Nucella*, show a marked tendency to eat mussels in the presence of spat and brood oysters When examining food preferences, the influence of environment and habit should be considered (Orton, 1929).

In the feeding experiment described on page 18, it was found that 20 *Urosalpinx*, offered equal numbers of oyster and *Crepidula* spat, devoured 752 oyster spat, but only 64 *Crepidula* spat, in 286 days. This confirmed field observations on the relationship between *Urosalpinx* and *Crepidula*, in the presence of oyster spat.

A sample of drilled oyster shells collected from Creeksea in 1953 (Hancock, 1954) showed that many oysters of three years and older had been drilled, together with many oyster spat. Measurement of the average diameter of these oysters showed that thirty-four at 30–39 mm., ninety-two at 40–49 mm., forty at 50–59 mm., seven at 60–69 mm., and one at 70–79 mm. had been drilled, thus including quite a high proportion of large oysters. Growth on this ground was never good, so that these oysters were probably older than their size implied.

Lucas (1947) has written of the ecological effects of metabolites, which he has termed 'ectocrines', the liberation of which may have an attractive or repulsive effect on other organisms. Bullock (1953) has extended this theory to include specific predator recognition by prey species. Carriker (1955) discussed the development of this concept applied to food preference in *Urosalpinx*. Experiments by Haskin (1940, 1950) showed that substances released by living oysters of varying ages have different degrees of attraction. Water from one-year-old oysters was more attractive than that from two-year-olds, which were in turn more attractive than oysters of three years and older. Cole (1942) was unable to show that *Urosalpinx* could detect the presence of food at distances as short as 35 cm., for the drills in his experimental trough moved at random. He did, however, observe that tingles showed a distinct preference for spat of thumb-nail size, not attacking very small spat until all the large spat had been destroyed.

Food preference experiments of the type performed by Stehouwer (1952) with *Aeolidia papillosa* (L.) have been attempted, but results have been complicated by the behaviour of *Urosalpinx*, which reorientates itself and moves against currents issuing from tanks containing no food. These experiments will be continued.

VI. SIZE-DISTRIBUTION AND GROWTH

The measurement most frequently used for the size of gastropods is the length or height of the shell from the apex of the spire to the tip of the siphonal canal. Cole (1942) examined the growth of *Urosalpinx* on British oyster beds in detail by shell-length measurements and examination of growth marks, and also established that females grow larger than males. Sex is determined by cracking the shell and examining for a penis. It is possible to see the sex of live animals by placing them operculum uppermost and observing them during their attempts to turn over. This method, however, takes much time and would not be suitable for a large sample.

1. GROWTH IN THE LABORATORY

This was studied in aerated seawater in 11-litre glass boxes. An equilibrium between encrusting algae and periwinkles was established, and the tingles were fed regularly on small brood and spat oysters and barnacles. A summary of the results is given in Table 4 and Fig. 12. The first juvenile tingles used hatched in the laboratory late in 1953. Only one individual survived the summer, and it measured 13 mm. at about one year old, and 15 mm. by the end of 1954 (Fig. 12(a)). Subsequent observations on this animal showed that

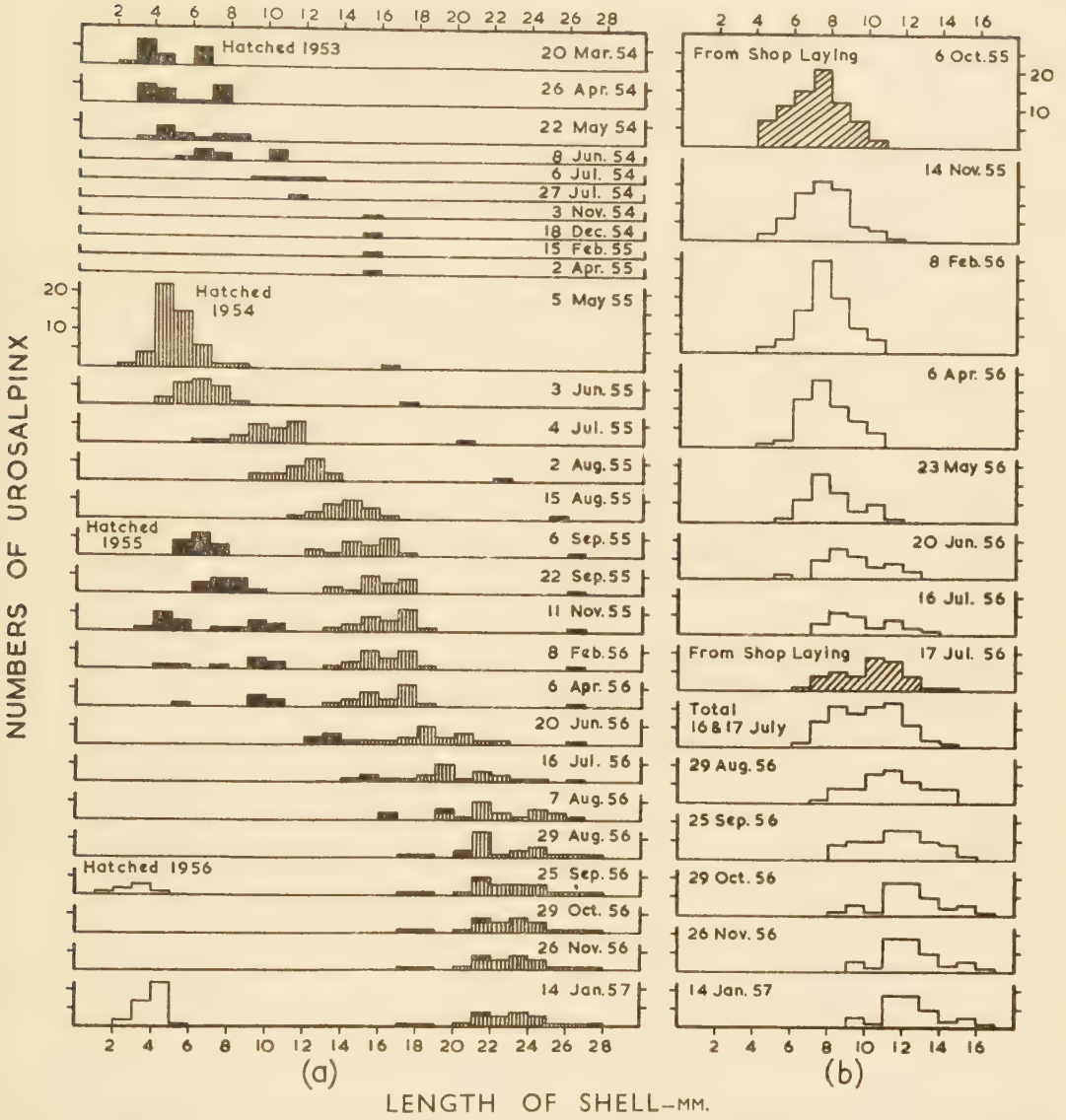


Fig. 12. *Histograms showing* (*a*) *growth of young* Urosalpinx *hatched in the laboratory* 1953–56 (*see Table* 4), *and* (*b*) *growth in the laboratory of* Urosalpinx *collected from the Shop Laying, River Roach, on* 6 *October*, 1955—*their size-distribution is compared with that of a further sample collected on* 17 *July*, 1956. *The two samples were mixed, and further growth studied.*

growth then ceased until the following spring, no substantial increment being recorded until the 5th May, 1955. By the 22nd September, 1955 it measured 26·5 mm., the greatest growth-rate being 0·17 mm. per day between 2nd–15th August. This tingle was a female and deposited 9 capsules early in September. Observations until the 14th January, 1957 showed that negligible growth occurred after spawning in September, 1955, though the lip of the shell remained unthickened. During the summer of 1956 it spawned normally.*

Another group of tingles hatched in the laboratory on the 27th July, 1954, and the largest of these measured 7 mm. at the end of the year. By the end of 1955 the tingles measured 14–18 mm. Growth occurred from May to September, and again the largest increment was added during the first half of August. At the end of 1956, the size-range

*This tingle died in the autumn of 1958. Growth after September, 1955, had been negligible, and the shell lip was partially thickened.

Table 4: *Growth of young* Urosalpinx *hatched in the laboratory*

Date measured	*Date hatched*							
	Late 1953		*Jul.* 54		*Oct.* 54		*Jul.* 55	
	Length (mm.)	*No.*	*Length (mm.)*	*No.*	*Length (mm.)*	*No.*	*Length (mm.)*	*No.*
20 Mar. 54	2–7	16						
26 Apr. 54	3–8	16						
22 May 54	4–9	13						
8 Jun. 54	5–11	10						
6 Jul. 54	9–12	4						
27 Jul. 54	11	1						
25 Aug. 54	13	1						
10 Sep. 54	15	1						
3 Nov. 54	15	1	up to 7	45				
18 Dec. 54	15	1	up to 7	45				
15 Feb. 55	15	1	up to 7	45	1–4	13		
2 Apr. 55	15	1	up to 7	45				
5 May 55	16	1	3–8	45	3–6	13		
3 Jun. 55	17·5	1	4–8	14	4–7	7		
23 Jun. 55	19·5	1						
4 Jul. 55	20·5	1	8–12	14	6–10	6		
2 Aug. 55	23	1	10–14	11	10–12	5		
15 Aug. 55	25	1	12–16	11	12–15	5	3–4	16*
6 Sep. 55	26·5	1	12–17	11	14–17	5	5–7	16*
22 Sep. 55	26·5	1	14–18	11	15–17	5	6–9	12*
11 Nov. 55	26·5	1	14–18	11	15–17	5	3–10	16
8 Feb. 56	26·5	1	14–18	11	15–17	5	4–10	8
6 Apr. 56	26·5	1	14–18	11	15–17	5	5–10	6
11 May 56 23 May 56	26·5	1	14–19	11	15–17	5	9–11	5
20 Jun. 56	26·5	1	15–22	11	17–19	5	12–14	5
16 Jul. 56	26·5	1	18–24	11	18–21	5	14–16	5
7 Aug. 56	26·5	1	18–25	11	19–21	5	16–19	3
29 Aug. 56	27·0	1	19–26	11	21–23	5	17–20	3
25 Sep. 56	27·0	1	20–26	11	22–24	5	17–21	3
29 Oct. 56	27·0	1	20–26	11	22–24	5	17–21	3
26 Nov. 56	27·0	1	20–26	11	22–24	5	17–21	3
14 Jan. 57	27·0†	1	20–26	11	22–24	5	17–21	3

*The smallest tingles of this group were not measured.
†In April, 1958, this individual, then rising five years old, had shown no further growth—its shell edge was partly thickened.

was 20–26 mm. Spawning took place during the year. This group, therefore, measured 10–14 mm. at one year old, and 18–24 mm. at two years of age. Some juveniles hatched later in 1954 (October), were kept for comparison. The largest of these always remained a few millimetres smaller than the largest of those hatched in July. Members of this group spawned throughout 1956, commencing in May when just nineteen months old.

Juveniles hatched early in 1955 showed a similar growth pattern. A group measuring 4–11 mm. taken from the Shop Laying, River Roach in October, 1955, was studied under similar conditions (Fig. 12(b)). The tingles were assumed to have been hatched during 1955. The largest of these added only 5 mm., that is by growing from 11 to 16 mm. in 1956, compared with an 11 mm. increase, from 10 to 21 mm., by the largest of the group hatched in the laboratory in 1955. The difference in growth-rate might be attributed in part to the larger number of Shop Laying individuals kept in one tank. Juveniles hatched late in 1956 measured 2–6 mm. by the end of 1956.

Under these conditions, therefore, young tingles reached 10 mm. (average 4–6 mm.) by the winter after hatching. Growth ceased from about September to April each year. At one year old they had grown to 16 mm. (average 12 mm.), and at two years old to about 24 mm. (average 21 mm.), perhaps reaching 25–26 mm. by the end of that year. Growth after spawning was limited. Although thickening of the shell edge did not occur during the year after first spawning at least, the onset of the spawning process seemed to be associated with a reduction in growth-rate. The tingles studied above were not sexed until the 14th January,

Table 5: *Growth-increments in millimetres of marked tingles liberated on 8 June, 1954 and recaptured from the Common Shore on the dates shown. 0 = negligible growth, – = slight decrease in length*

Date recaptured	*Length of* Urosalpinx *when liberated (mm.)*										
	24	25	26	27	28	29	30	31	32	33	34
3 Aug. 54			0								
15 Nov. 54				0			2				
19 Nov. 54		0	0	0, 0		0, 0, 0					
1 Dec. 54				0				–	0		
12 Mar. 55						0	0	0			
6 May 55		0		0		0					
9 May 55		0	–	0, 0, 0, 0, 0, -	0	0, 0, 0	0, 0, 0, 0	0, 0	0		
24 May 55			0	1, 0	0, 0, 0	0, 0, –	–	–	0, 0		
7 Jun. 55	1				0, 0, 0, 0	0, 0, 0, –	0, 0, 0, 0	0, 0, 0, –	0		
22 Jun. 55			0, 0, 0, –	0, 0, 0, 0, 0, 0	0, 0, 0, 0, 0, 0	1, 0, 0, 0, 0, 0, 0	0, 0, 0, 0, 0, 0, 0	0, 0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0, –	0
				0, 0, 0, 0, 0, 0	0, 0, 0, 0, 0, 0, 0	0, 0, –, –, –, –	0, 0, 0, 0, 0, 0	0, 0, –, –, –			
7 Jul. 55		0		0, 0, 0	1, 0, 0	0, 0, 0, 0, 0	0, 0, 0, –, –	1, 0, 0, 0, –			0, 0
						0, 0, 0, 0, 0					
21 Jul. 55			0			1, 0, 0, 0, 0					
5 Aug. 55		2		1		3, 1	0, 0			0	
19 Aug. 55		1				0					
5 Sep. 55							2	3			
20 Sep. 55						2					
5 Oct. 55						2		1			
27 Apr. 56									1		
14 May 56				3		1, 1	3	1			
25 May 56									2		
9 Jul. 56						2, 0					
8 Aug. 56	2										
Total number of growth increments recorded	2	6	9	30	24	54	34	28	11	6	4

1957, when it was found that the females were the largest in each group, but they had not grown so much faster that males and females of one age-group became widely separated. The tingles described are being retained for future observations.

A group of tingles transferred from an oyster bed to the laboratory on the 31st August, 1954, measuring 9–25 mm., showed a rather lower growth-rate. By October, 1955, the maximum growth-increment recorded was 4 mm., but the average increment was only 1·5 mm. Again the maximum growth occurred in July and August, but none during the winter. A group of tingles measuring 24–34 mm., used in a feeding experiment and fed with plentiful supplies of oyster spat, showed negligible growth between March and the end of August, 1954. It is possible that a change of environment has a retarding effect on growth-rate, but since all these tingles were mature, it may have been due to the post-spawning reduction in growth.

2. GROWTH OF MARKED TINGLES

Tingles, marked for the migration experiment at the Common Shore on the 8th June, 1954, were measured when recaptured. The original length of each tingle was known from the combination of paint colours used, and the growth increment could be recorded. The results for 208 tingles measured after recapture from the 3rd August, 1954 onwards are shown in Table 5. Recaptures in 1954 were small and indicated little growth, as did most of those recaptured by July, 1955. Later, in August-September, 1955 and in 1956, growth-increments of up to 3 mm. were recorded, but length-increases were normally small and rather variable. Decreases in length were sometimes recorded (Table 5); these would be mainly due to the breakage of the tip of the siphonal canal, which occurs frequently in nature. No attempt was made to distinguish between sexes, but since the sample for marking was taken from tiles at the Common Shore, it would have included about 60% females.

3. VARIATION OF SIZE-RANGE WITH DISTRIBUTION

The importance of localised sampling for growth studies must be emphasized. Measurement of samples from different, yet quite close, localities, has revealed surprising differences in size-distribution. Fig. 13 shows population histograms of females from different localities in the Rivers Roach and Crouch. The maximum and the peak modal sizes are smallest at the Southward Laying and largest in Paglesham Reach. The largest *Urosalpinx* recorded in this country, a female measuring 47 mm., was dredged in Paglesham Reach. The Shop Laying is the northern shore of Paglesham Reach, and there the size-distribution is similar to that at the Common Shore where similar ecological conditions exist. At Creeksea, larger tingles were found than at the Southward Laying although the two oyster grounds are in the same river and separated by only 2–3 miles.

Carriker (1955) compared the records by various workers of maximum sizes of *Urosalpinx* in different geographic regions, and tentatively suggested that three different sizes of drill exist, the giant American form of maximum height, 51–61 mm., the English form, 39–43 mm. and the small widespread American form, 26–40 mm. Engle (1942), using controlled laboratory conditions, showed that groups of *Urosalpinx*, fed separately on different foods, showed great variation in rates of growth. He found that tingles fed on *Mya* grew most rapidly, the growth-rate decreasing on oysters, barnacles and mussels respectively. Smith (1940) showed that the starfish *Asterias forbesi* grew much more rapidly when fed on mussels than on oysters. Evidently the kind of food eaten has some influence on growth-rate. It has been suggested that temperature (Fraser, 1931) and latitude have an effect on size-distribution (summarised by Carriker, 1955), but these would not account for such local variations. Mistakidis (1951) showed that depths in the Shop Laying/Paglesham Reach area varied from 0–6 m. at L.W.O.S.T. on the Shop Laying to 0–6·8 m. in Paglesham

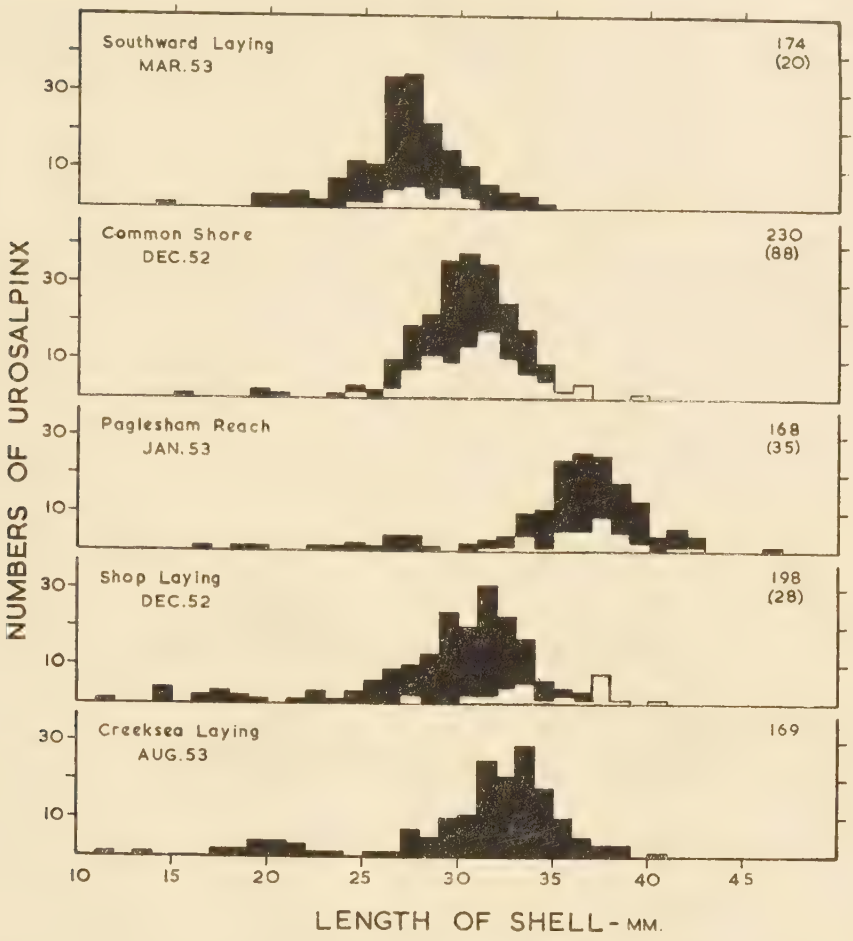


Fig. 13. *Size-distribution of female* Urosalpinx *from different oyster grounds in the Rivers Roach and Crouch. The numbers with thickened shell lips are shown in white (not examined in Creeksea Laying sample). The total in each sample is shown in the top right-hand corner of each histogram, with the numbers with thickened shells in brackets. Shell lengths have been grouped at 1-mm. intervals.*

Reach. The north shore is, however, hard so that there is a considerable shoreward-moving population on the Shop Laying. The south shore is of soft mud and shelves more steeply, so that the Paglesham Reach population is a fully submerged, deeper-water population. Oyster spatfall is usually much better on the Shop Laying than the Southward Laying, and poor in Paglesham Reach (G. D. Waugh, personal communication). Mistakidis (1951) showed also that barnacles are plentiful on the Shop Laying, but scarce in Paglesham Reach, so that tingles there cannot feed on the normal diet of oyster spat and barnacles, but would require to feed on larger organisms, oysters, *Crepidula*, etc. The size of spawn capsules and the range of the numbers of eggs per capsule are also larger in Paglesham Reach than elsewhere (Figs. 21 and 22); young tingles are represented normally in the population, but it is significant that none of the smaller sizes of capsule is present. Since capsule size is directly related to the size of the parent, this implies no spawning by the younger individuals. Increased growth may well, therefore, result from delayed maturity. Similarly, the small range of size-distribution at the Southward Laying could result from an early maturity. Thickening of the lip of the shell, which results from cessation of growth and occurs some time after spawning, begins earliest at the Southward Laying and latest at

Paglesham Reach (Fig. 13). The factors responsible for determining the onset of maturity are somewhat obscure, but it is felt that the clue lies in the feeding habits of the different populations.

4. GROWTH FROM SIZE-DISTRIBUTION

Samples collected from tile traps at the Shop Laying (Fig. 14) are of particular interest, because the smallest size-groups were not represented in Cole's (1942) samples. Small tingle sare difficult to obtain by dredging because they are lost through the meshes. Limited numbers were obtainable from tiles only towards the end of each year. The samples shown in Fig. 14 were not sexed, but, in view of the laboratory results already described, it was felt that this would not interfere with the identification of the first few year-groups; also samples for the 19th September–18th November, 1955, were added together since, as laboratory results show, growth in the field during this period was unlikely. The first size-group, hatched in 1955, showed a mode at 7 mm., and a range of 4–11 mm. Subsequent

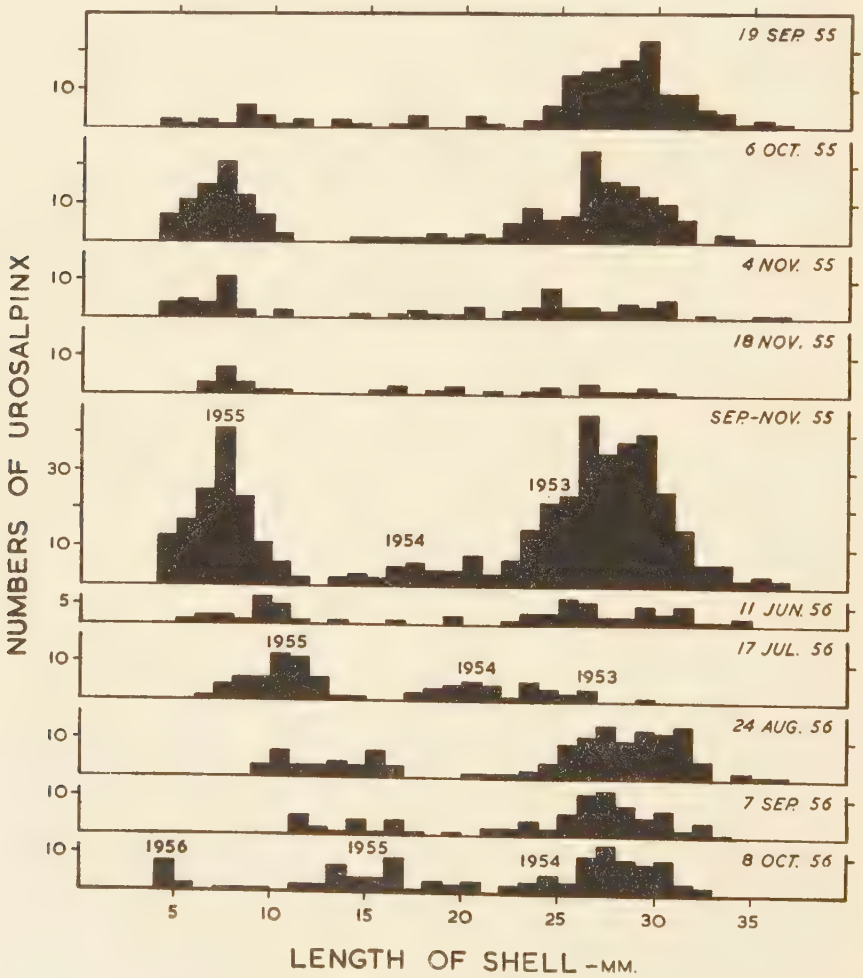


Fig. 14. *Size-distribution of* Urosalpinx (*not sexed*) *from the Shop Laying, River Roach. Samples taken September–November,* 1955 *have been added together* (*see text*). *The year of hatching is shown at the approximate mean size of each year-group. Shell lengths have been grouped at* 1-*mm. intervals.*

samples showed a steady progression of the year-groups until by the end of 1956, a new group (hatched 1956) had appeared at 4–6 mm. 1955-hatched tingles now occupied the 11–20 mm. range; the next group (hatched 1954) was centred around a mode of about 24 mm., and the next group around 27 mm. These results agree very well with those

Table 6: *Size-distribution of female* Urosalpinx *in samples collected from tile traps at the Common Shore, River Roach*, 1954–1955

Shell length (mm.)	*Date of collection*										
	3 Jun. 54	2 Jul. 54	3 Aug. 54	31 Aug. 54	29 Sep. 54	1 Nov. 54	7 May 55	22 Jun. 55	21 Jul. 55	19 Aug. 55	5 Sep. 55
9·0				1							
9·5				–							
10·0				1							
10·5				1							
11·0				2							
11·5				1							
12·0				1							
12·5				1							
13·0			1	3							
13·5			–	1							
14·0			–	–	1						
14·5			–	1	–						1
15·0		1	–	–	1	1				1	1
15·5		–	–	–	–	1				–	–
16·0		–	1	–	2	–				–	–
16·5		–	–	1	–	2				–	–
17·0		–	–	1	–	–				–	–
17·5		–	–	–	–	1				–	–
18·0		–	–	–	–	1				–	–
18·5		–	–	1	–	1				–	–
19·0		–	–	–	1	1				1	1
19·5		–	–	–	–	–				–	1
20·0		–	1	–	2	1	1			2	–
20·5		–	–	–	1	1	–			–	–
21·0	1	–	–	–	2	–	–			–	–
21·5	–	1	1	1	1	–	–			–	–
22·0	2	1	1	1	–	1	–			1	–
22·5	–	2	–	–	1	–	1	2		–	1
23·0	5	2	3	–	1	–	1	1	2	2	1
23·5	1	–	–	–	–	–	–	–	3	–	1
24·0	3	6	2	–	1	–	–	2	–	3	5
24·5	6	1	1	3	3	3	1	–	–	1	–
25·0	10	6	3	2	6	3	–	2	–	2	2
25·5	12	9	8	4	5	1	4	10	–	1	3
26·0	14	14	7	5	7	6	7	11	6	2	2
26·5	13	11	14	7	8	2	3	24	7	4	1
27·0	28	25	17	7	12	3	9	24	4	10	5
27·5	30	32	23	6	15	7	9	29	5	8	5
28·0	33	30	18	19	16	4	9	29	9	18	2
28·5	41	27	22	9	16	4	10	29	10	11	7
29·0	49	33	17	15	16	5	14	28	12	8	12
29·5	46	27	12	8	15	3	12	18	11	9	9
30·0	34	19	14	7	17	3	9	37	10	9	8
30·5	28	29	14	2	18	4	15	37	12	11	5
31·0	29	12	3	9	16	7	7	34	11	9	8
31·5	21	8	10	3	10	1	10	18	18	6	5
32·0	17	11	7	2	6	1	6	15	6	4	8
32·5	9	4	3	3	8	1	4	18	4	7	6
33·0	6	4	3	2	8	–	3	8	5	4	6
33·5	10	3	3	2	1	1	2	10	–	1	3
34·0	2	2	1	3	2	–	2	10	1	–	1
34·5	2	2	2	1	1	1	3	1	–	1	1
35·0	–	1	1		2	–	1	2	1		–
35·5	1	1	1		–	–	1	1			1
36·0	1	–	1		–	–	–	–			1
36·5	–	–			1	–	–	–			
37·0	1	–			–	1	–	–			
37·5		–			–		–	1			
38·0		–			1		–	2			
38·5		1			3		1	1			

Table 7: *Size-distribution of male* Urosalpinx *in samples collected from tile traps at the Common Shore, River Roach,* 1954–1955

Shell Length (mm.)	*Date of collection*										
	3 Jun. 54	2 Jul. 54	3 Aug. 54	31 Aug. 54	29 Sep. 54	1 Nov. 54	7 May 55	22 Jun. 55	21 Jul. 55	19 Aug. 55	5 Sep. 55
12·0					1						
12·5					–						
13·0					–						
13·5				1	–						
14·0				–	–						
14·5				–	1						
15·0				–	–						
15·5				–	1	–					
16·0				–	–						
16·5				–	–	1					
17·0			1	–	–	–				1	
17·5			–	1	1	–		1		–	
18·0	1		–	–	2	–		–		–	1
18·5	–		–	1	1	–		–		–	2
19·0	–		–	1	3	–		–		–	–
19·5	–		–	–	2	2		–		–	–
20·0	–		–	–	1	1		–		–	–
20·5	2	1	–	–	–	–	1	–		2	1
21·0	–	3	–	–	3	–	–	–		–	–
21·5	–	1	–	2	–	1	–	1		2	–
22·0	–	–	–	1	4	–	–	–		–	–
22·5	–	–	–	1	2	1	–	–		2	4
23·0	3	1	1	3	–	2	–	–		–	1
23·5	–	2	1	–	3	–	–	–		–	1
24·0	2	4	1	–	4	–	3	1		–	1
24·5	4	1	3	5	4	1	1	–		–	2
25·0	11	7	5	1	3	1	2	3	1	1	1
25·5	6	10	7	4	4	3	4	9	–	–	4
26·0	13	15	5	8	6	6	3	9	–	–	1
26·5	16	13	12	8	8	3	7	14	2	7	4
27·0	14	19	10	13	17	5	13	19	2	5	3
27·5	19	23	11	13	13	3	8	21	4	4	1
28·0	19	21	14	12	18	5	12	15	6	8	11
28·5	19	17	20	7	7	1	15	25	5	4	9
29·0	11	19	17	13	15	2	4	15	5	7	8
29·5	15	17	11	9	10	1	6	18	8	5	8
30·0	18	17	14	6	12	4	7	20	3	9	13
30·5	14	20	7	6	13	1	4	7	4	12	8
31·0	8	12	5	1	5	1	3	9	3	10	6
31·5	3	4	2	1	7	–	4	5	2	1	6
32·0	8	2	3	–	3	1	1	5	2	1	5
32·5	3	–	1	1	3		1	4	2	2	1
33·0	1	1	2	–	3		–	4	2	1	–
33·5		2	–	2	–		1	–		2	3
34·0		1	–	–	1			–		–	–
34·5		–	–	–	1			–		1	–
35·0		–	–	–	1			1			–
35·5		–	–	1	1			1			2
36·0		–	–		–			–			
36·5		–	–		–			–			
37·0		1	–		1			–			
37·5			–					1			
38·0			–								
38·5			–								
39·0			1								

obtained in the laboratory (Table 4). Further evidence of the growth of 1955-hatched tingles was obtained by taking the group measuring 4–11 mm. from the 6th October, 1955 sample, and following their growth in the laboratory (Fig. 12(b)). On the 17th July, 1956, the measurements of the survivors agreed well with those from an additional Shop Laying sample (Figs. 12(b) and 14). These also were retained in the laboratory.

Young tingles occurred less often in samples from tile traps at the Common Shore (Tables 6 and 7). The analysis of several samples using probability paper (Harding, 1949;

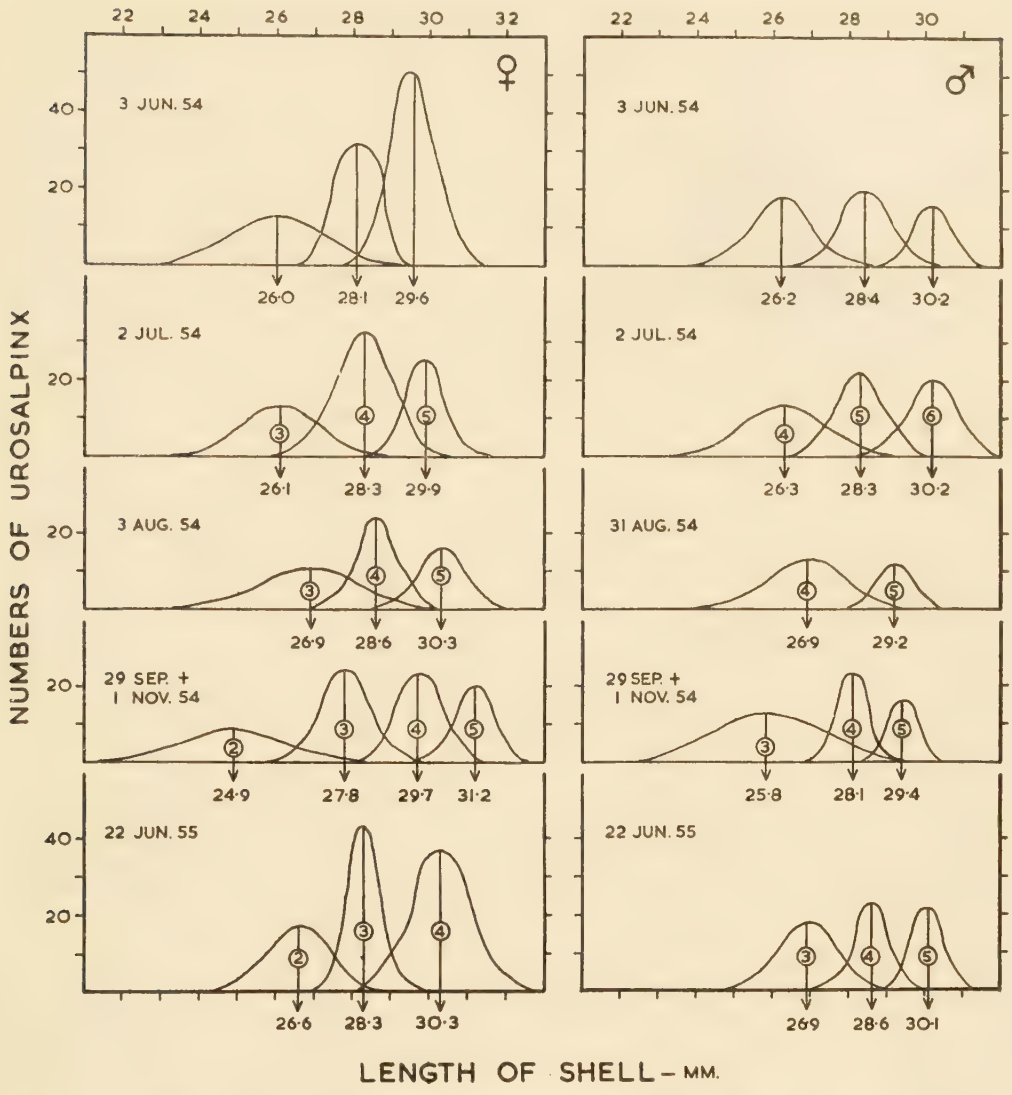


Fig. 15. *The analysis, using probability paper, of samples of* Urosalpinx *from tile traps at the Common Shore (see Tables* 6 *and* 7*). Year-groups are shown by normal curves with the appropriate age in a circle; mean shell lengths are indicated by arrows.*

Cassie, 1954; A. C. Burd, personal communication) showed the positions of normal curves representing different year-groups (Fig. 15). Close overlapping of older year-groups, which were poorly represented in the samples, rendered them inseparable by this method.

Resolution of the sample of females taken on the 2nd July, 1954, showed three year-groups, which, from knowledge of growth at the Shop Laying and in the laboratory, must be 3, 4 and 5 years of age respectively. Corresponding groups in the male sample taken on the same date had slightly higher means, and were concluded to represent tingles of 4, 5 and 6 years of age. The year-groups could be traced through subsequent samples, until the 22nd June, 1955, when the growth in one year of any group was found to be of the same order as the increment between means of successive groups. Annual growth-increments generally decreased slightly with age.

Additional confirmation of this estimate of the growth pattern of *Urosalpinx* was obtained by applying von Bertalanffy's (1938) growth equation to the data obtained from the combined results of observations on growth in the laboratory, and at the Shop Laying and

Common Shore. The following estimate of length-at-age was used:—

Age (years)	*Mean length (mm.)*	
1	12	
2	21	
3	26·1	from Common Shore sample, 2nd July, 1954 (Fig. 15).
4	28·3	
5	29·9	

This was plotted in Fig. 16, to give the usual shape expected of a growth curve following this growth equation. A straight line was obtained (Fig. 17) by plotting the mean length at one age (L_{t+1}) against that of the previous year-group (L_t). Its intercept with the 45° line representing no change in size (i.e. $L_{t+1} = L_t$) lay at 31·5 mm. This value (L_∞) is the mean size to which *Urosalpinx* at the Common Shore can be expected to grow. The various parameters of von Bertalanffy's equation were calculated, and these growth data were shown to fit the equation well, giving a value of 0·617 for K, the coefficient of catabolism.

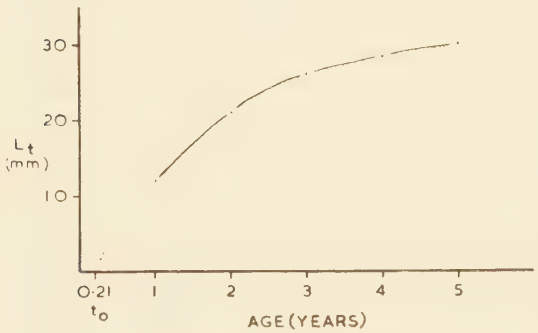


Fig. 16. *Growth curve of* Urosalpinx *for the first five year-groups. L_t is mean shell length-at-age; t_0 is a parameter of von Bertalanffy's growth equation (see text).*

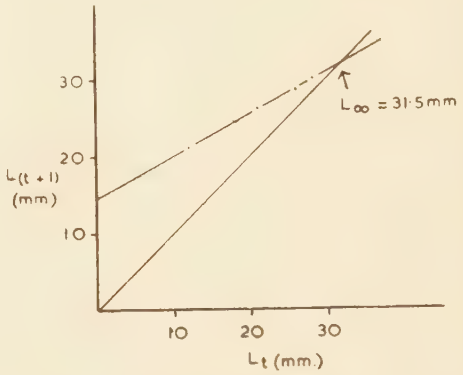


Fig. 17. *Relationship between the mean shell lengths of pairs of year-groups. L_∞ is a parameter of von Bertalanffy's growth equation (see text).*

Reference to the size-distribution of samples from the Common Shore (Fig. 13 and Table 6), shows that 31·5 mm. is a reasonable value for L_∞. Tingles as small as 24 mm. have been taken at the Common Shore (Fig. 13) with partial thickening of the lip of the shell, indicating that growth of some individuals had virtually stopped at this size. Moore (1936) showed that, in *Nucella*, maturity is accompanied by cessation of growth and thickening of the lip of the shell. Similar thickening of the shell lip does occur in *Urosalpinx* (Fig. 13). On the 20th August, 1953 however, 22 of 23 tingles taken in the process of spawning had normal non-thickened shells, and in many similar observations, unthickened *Urosalpinx* were seen to be spawning. An individual hatched in the laboratory in 1953 (Table 4), which spawned in 1955 and 1956, was still unthickened in February, 1957, but there was little growth after spawning. Evidently, in *Urosalpinx* the growth-rate is considerably reduced after spawning, and, in a proportion of the population, growth may cease entirely and be followed by thickening of the shell lip.

At the Common Shore and Shop Laying, therefore, the mean growth-increments of females appear to be:—1st year, 12 mm.; 2nd year, 9 mm.; 3rd year, 5 mm.; 4th year, 2 mm.; 5th year, 1–2 mm. The size-distribution of dead shells collected by dredging at the Common Shore (Fig. 18), suggests that the highest mortality occurs at shell lengths of 28–32 mm., i.e. among tingles of about 5 years of age, but obviously a large proportion of the population grows to be much older than this. The size-distribution of groups above 5 years of age was too complicated by post-spawning reduction of growth rate and shell-thickening, for analysis. At the Southward Laying, where shell thickening occurs earlier, the value for L_∞ would be lower. In Paglesham Reach, growth is evidently more extended,

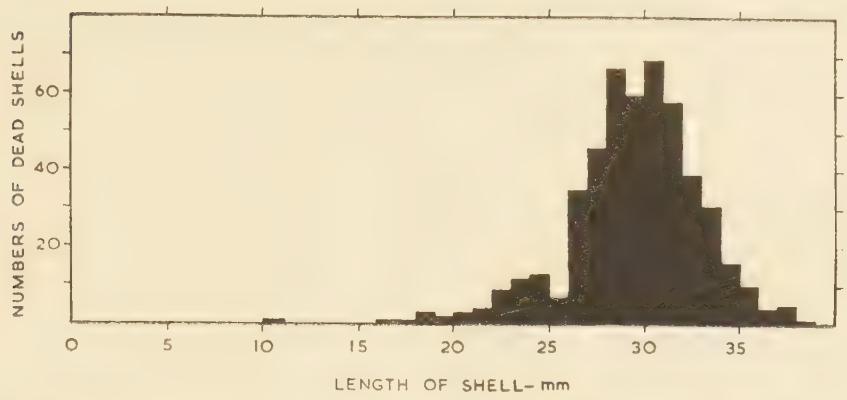


Fig. 18. *Size-distribution of dead shells of* Urosalpinx *collected by dredging at the Common Shore, River Roach.*

shell-thickening commences later (Fig. 13) and L_∞ would be higher. Cole's (1942) growth estimates were based on samples from the River Blackwater, and the size-distribution resembled that of tingles taken from Paglesham Reach rather than from the Common Shore. Growth of female tingles is, however, very similar in the two sets of observations, with the exception of the first year, in which growth by Cole's estimate was much higher. If growth on these two grounds were comparable, it might appear that one of the early year-groups, which were poorly represented in Cole's samples, had been overlooked, but since obviously

Table 8: *Percentage females in total catches of* Urosalpinx *from the Common Shore, River Roach*

Date	*Method of collection*	*% Females*	*Total number in catch*
12 Sep. 52	Power dredge	52·0	173
12 Sep. 52	Tingle dredge	51·7	58
7 Oct. 52	Power dredge	48·1	243
7 Oct. 52	Tingle dredge	48·4	190
11 Nov. 52	Power dredge	52·7	36
11 Nov. 52	Tingle dredge	46·7	92
5 Dec. 52	Power dredge	44·7	38
5 Dec. 52	Tingle dredge	41·7	36
6 Mar. 53	Power dredge	54·0	100
8 May 53	Power dredge	61·2	129
8 May 53	Tingle dredge	55·6	142
8 May 53	Tile traps	62·8	148
3 Jun. 53	Power dredge	62·9	248
3 Jun. 53	Tingle dredge	65·0	143
19 Jun. 53	Tile traps	72·9	74
1 Jul. 53	Tile traps	64·8	310
14 Jul. 53	Power dredge	58·0	138
14 Jul. 53	Tingle dredge	41·7	120
22 Jul. 53	Power dredge	60·9	238
22 Jul. 53	Tingle dredge	60·8	240
27 Aug. 53	Power dredge	51·1	47
12 Sep. 53	Tile traps	59·5	247
29 Sep. 53	Power dredge	43·1	58
29 Sep. 53	Tingle dredge	56·1	41
13 Nov. 53	Power dredge	41·7	48
13 Nov. 53	Tingle dredge	42·9	21
5 May 54	Tile traps	66·9	178
3 Jun. 54	Tile traps	68·1	665
2 Jul. 54	Tile traps	58·1	559
3 Aug. 54	Tile traps	58·2	369
31 Aug. 54	Tile traps	51·0	233
1 Nov. 54	Tile traps	61·0	118

greater growth occurs on the grounds studied by Cole, early growth may have been more rapid. As in Cole's observations, males in this investigation were found to be 1–2 mm. smaller than females of the same year-group.

5. SEX-RATIO

Cole (1942) has discussed in detail the factors influencing the ratio of males to females in tingle catches taken by dredging and hand-picking on the shore. Knight-Jones and Waugh (personal communications) found that of tingles attached to rocks, there was a marked tendency for the males to be dislodged more easily by sudden jarring. This observation would help to explain the normally higher percentage of females occurring in dredged catches. Table 8, showing the percentage females in catches of power dredges, tingle dredges (see p. 52) and tile traps (p. 53), confirms that percentages of females are highest in summer, especially June, and lowest, often below 50% in winter. The highest percentages of females were taken from tile traps.

VII. BREEDING

The two sexes are separate, and the female grows to a larger size than the male. Male and female are readily distinguished by the presence of a large curved penis just behind and to the right of the right tentacle in the male, which also has a whitish gonad compared with the orange-yellow gonad of the female (Federighi, 1931). Thread like (eupyrene) and worm-like (apyrene) forms are represented in the spermatozoa. The worm-like form is 35μ and much broader than the thread-like form which is 170μ in length.

The eggs of *Urosalpinx* are usually between 0·3 and 0·4 mm. in diameter and are deposited in capsules attached individually to the substratum in groups. The form of the egg capsules has been described by Orton and Amirthalingam (1929) and compared with those of the similar capsules deposited by *Nucella* and *Ocenebra*. Fretter (1941) has also described the structure, method of formation and deposition of the egg capsules of *Nucella* and *Ocenebra*. The structure of the capsule of *Urosalpinx* has been described separately (Hancock, 1956) in relation to the hatching process. Each is yellow, tough and vase-shaped, and attached to the substratum by a narrow stalk (Frontispiece). The young emerge from the capsules as fully-formed juvenile tingles, usually 1–2 mm. in length.

1. COPULATION

Carriker (1955) reported that copulation had not been observed in *Urosalpinx*, but Stauber (1943) described a laboratory observation on *Eupleura caudata*, its close relative in America. *Urosalpinx* in the process of copulation have now been observed in the laboratory on several occasions. On the 24th March, 1954, at a temperature of 9–10°C., a male of 32 mm. length and a female of 28 mm. were found in the copulating position on the side of a laboratory tank. The female was attached to the side of the tank with the tip of the siphonal canal pointing diagonally downwards to the left. The male was attached to the female only and pointing in the opposite direction, their shell apertures being apposed. When separated, the extended penis of the male was withdrawn from the female. A second pair of tingles, male 33 mm. and female 30 mm., were seen in a similar position on the 26th March, 1954 (temperature 8–9°C.) the female subsequently commencing to spawn on 6th May. This female was not observed to feed before copulation, but consumed several oyster spat before

commencing oviposition. A further pair were observed on the 2nd April, 1955, the temperature being 8°C., having previously reached 11°C. during March. Under laboratory conditions, it appears as though copulation takes place at a temperature near to that at which feeding commences, about five weeks before oviposition. The female drill isolated by Stauber (1943) from the 9th April to 21st October, which deposited fertilised eggs, could have been fertilised in the spring before capture, and his observation does not necessarily suggest that the sperm remains viable for long periods. Observations on *Ocenebra* showed that seven females isolated for two years with three males, all produced viable spawn in both years, indicating some degree of polygamy.

2. AGE AT MATURITY

Experiments made by Cole (1942) suggested that females below 25 mm. in length at the beginning of the season deposit a small number of egg capsules. He estimated that they were two years old. Pope (1910–11) found that females of 13 mm. length, believed to be one year old, deposited egg capsules, and Stauber (1943) showed that of drills of 11–15 mm. at the beginning of the season, none spawned until October, when one cluster of capsules was found.

A female tingle hatched in the laboratory late in the summer of 1953 was isolated with some tingles hatched on the 27th July, 1954. No spawn was found in the tank until early in September, 1955, when four small capsules were deposited. The tingle was then two years of age and measured 26 mm. in length, compared with 16 mm. at the beginning of the season. These capsules contained eggs which remained undeveloped. At the beginning of October, a further five capsules were deposited next to the first four. These soon commenced to develop normally, indicating that the tingle must have been fertilised by one of several males, fourteen months old and 14–17 mm. long. It seems likely that copulation with a newly-matured male took place between the first and second spawnings, and it is clear that unfertilised females do lay spawn. A limited number of capsules always fail to develop in the field during the season, and often these are found together in a group as if laid by one female. Tingles hatched in the laboratory in October, 1954 commenced depositing capsules on the 23rd May, 1956, at nineteen months old. The group included three females, 15–17 mm. long, the largest of which was believed to have commenced spawning first, and two males of 16 mm. that had fertilised the females. All of the capsules produced young.

3. SPAWNING PERIOD

Cole (1942) showed that *Urosalpinx* deposited its spawn in the River Blackwater from May to September, the greatest numbers being found in May–June, with only a few fresh capsules in August–September. He estimated that spawning commences each year in British waters when the sea temperature reaches 12–13°C. Carriker (1955) has shown that the temperature required for oviposition varies in different geographic regions.

Recent observations on the relation between temperature and the deposition of capsules in the Rivers Roach and Crouch, and in the laboratory, are shown in Table 9. The lowest temperature for oviposition was 11–12°C. both in the laboratory and in the field in 1954, but in general the temperatures agree well with Cole's estimate. It appears as though spawning on the shore follows a sharp rise in air temperature, which would be transmitted at once to individuals exposed at low water. Submerged populations will respond only subsequently as the water temperature rises. For example, on the 7th May, 1955, on the Shop Laying, substantial numbers of capsules were present on tiles on the shores but very few were taken by dredging.

The total numbers of capsules taken in standard dredge hauls during surveys of the Common Shore, River Roach, in 1953 and of the Southward Laying, River Crouch, in

Table 9: *Incubation periods of* Urosalpinx *capsules*

Location	*Date fresh capsules first seen*	*Temp. reached (°C.)*	*Date first seen hatching*	*Incubation period (days)*	*Temp. range (°C.)*	*Average temp. (°C.)*
Shop Laying	7 May 53	13	8 Jul. 53	62	13–22	15·9
Common Shore	8 May 53	13	5 Jul. 53	58	13–22	15·9
Southward Laying	12 May 53	13–14	9 Jul. 53	58	13–22	NR
Laboratory	30 Oct. 53*	–	5 Jan. 54	67	13–7	10·5
Shop Laying	5 May 54	11–12	NR			
Common Shore	5 May 54	11–12	After 2 Jul. 54	>58	11–20	NR
Southward Laying	13 May 54	NR	After 2 Jul. 54	>58	11–20	NR
Laboratory	30 Apr. 54	11	After 9 Jul. 54	>70	11–19	15
Common Shore	25 Apr. 55	12–13	NR			
Laboratory	28 Apr. 55	13	6 Jul. 55	69	12–21	15

*Spawn was observed for the first time each year on the dates shown except for this group.
NR—Not recorded.

1955, are shown in Fig. 19, all capsules from freshly deposited to hatched being included. From Tables 12 and 13, it can be seen that at the Southward Laying, although the greatest quantity of spawn was found on the 29th July, more than two-thirds of the total spawn had already been deposited before 18th July and some had already hatched. The total quantity of spawn dredged fell considerably after the 26th August due to the disintegration of capsules, so that the proportion of hatched capsules was in reality much larger after that date. Table 11 shows that in the same year (1955) at the Common Shore, more spawn was deposited later in the season than at the Southward Laying. Fresh spawn was dredged as late as the 25th November from the Southward Laying (Table 12), thus extending Cole's (1942) estimate of the breeding period by two months. A little fresh spawn was taken on tile traps at the Common Shore in November, 1953, 1954 and 1955 and also by Waugh (personal communication) from wire bag traps in November, 1949 and 1950. The fate of capsules deposited late in the season has been discussed (Hancock, 1956). It was demonstrated that a low temperature of 5° C. kills the egg stage, but only inhibits development and hatching in subsequent stages. A limited number of capsules containing live advanced stages have been taken early in each year before the normal breeding period. It appears that capsules can survive even a very cold winter in a retarded state to continue their development and hatch in the following spring.

The extent of the period of oviposition can better be seen by reference to Fig. 26, showing the total numbers of fresh capsules taken fortnightly from 225 tile traps placed at L.W.O.S.T. on the Shop Laying, River Roach in 1955 and 1956 and 200 at the Common Shore, River Roach in 1954 and 1955. Numbers given are of capsules actually taken off at each visit, and therefore freshly deposited in the previous fortnight, thus showing the extent and intensity of the breeding period at L.W.O.S.T. It must be remembered, however, that at each visit some adult tingles (see Figs. 24 and 25) were removed, and these would normally have added to the intensity of subsequent spawning. The graphs obtained for the Shop Laying and Common Shore in 1955 appear very similar, although the collections in June are not comparable. On the Shop Laying, an insufficiently low tide prevented collection on the 7th, so that the figure for the 25th (shown by a broken line in Fig. 26) is very high, representing deposition over a period of one month (this figure would also be influenced by the non-removal of adult tingles for one month, and the possibility of increased gregariousness over a longer period) and on the graph for spawn collected from the Common

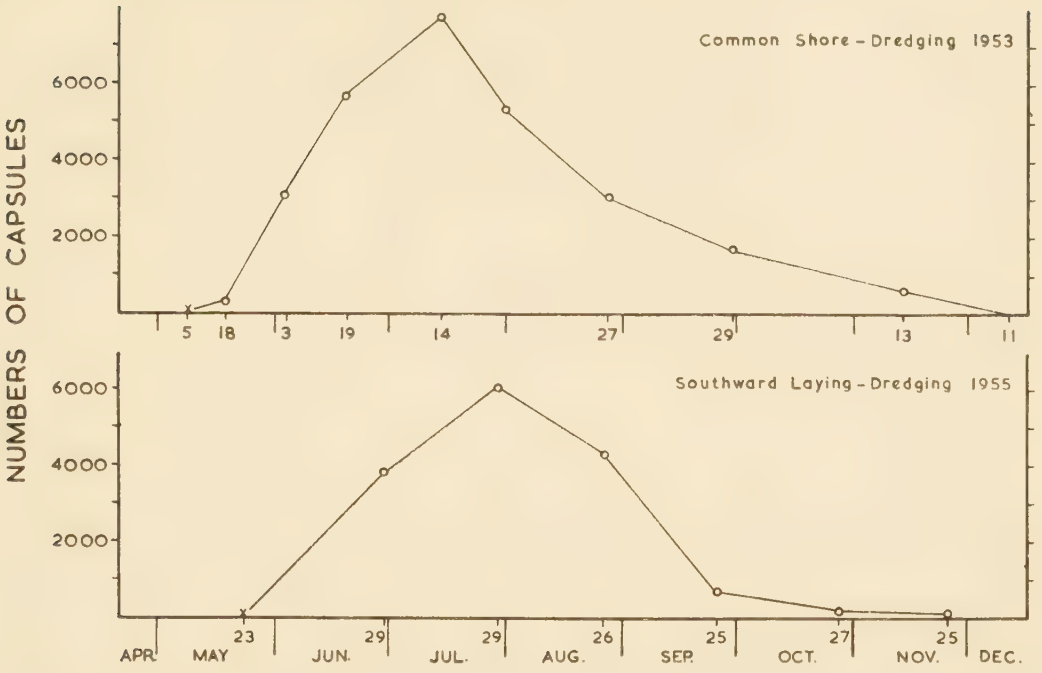


Fig. 19. *Numbers of* Urosalpinx *capsules taken on each date during dredge surveys (see text) at the Common Shore, 1953, and Southward Laying, 1955. Points marked* (x) *indicate capsules present but less than* 100.

Table 10: *Percentages of full and empty* Urosalpinx *capsules in samples dredged from the Common Shore in* 1953

Date	*Freshly deposited* %	*Developing* %	*Hatched* %	*Total capsules on 50 objects*
27 Aug. 53	13·3	46·1	40·6	2360
29 Sep. 53	5·5	20·5	74·0	1875
13 Nov. 53	1·8	15·0	83·2	1995

Table 11: *Percentages of full and empty* Urosalpinx *capsules in samples dredged from the Common Shore in* 1955

Date	*Freshly deposited* %	*Developing* %	*Hatched* %	*Total capsules on 50 objects*
9 Jul. 55	50·3	42·4	8·3	2837
4 Aug. 55	17·7	51·7	30·6	2161
19 Aug. 55	8·7	50·7	40·6	2207
6 Sep. 55	10·3	46·2	43·5	2153

Table 12: *Percentages of full and empty* Urosalpinx *capsules in samples dredged from the Southward Laying in* 1955

Date	*Freshly deposited* %	*Developing* %	*Hatched* %	*Total capsules on 50 objects*
18 Jul. 55	28·5	70·3	1·2	1580
12 Aug. 55	11·8	47·1	41·1	1672
26 Aug. 55	2·2	30·5	67·3	1706
9 Sep. 55	0	20·8	79·2	938
25 Sep. 55	0	19·6	80·4	561
25 Nov. 55	2·7	5·7	91·6	191

Shore in 1955, two collections have been omitted, because although the spawn was removed, interference with the tiles had invalidated the results. At the Common Shore in 1954 a rather different graph was obtained. Spawning commenced slightly later but reached maximum intensity more quickly and continued at a high level for a period of 9–10 weeks before dropping rather sharply, whereas in 1955 the decrease in intensity was less rapid and rather more capsules were deposited in August and September. It is believed that the variation in rate of deposition of capsules on the shore is influenced by temperature, but there is insufficient evidence for a full correlation.

Adult tingles kept in the laboratory in 1954 spawned mainly in May, with limited spawning in June–July. One two-year-old tingle, at first spawning, deposited a limited number of capsules in September. Another group of two-year-olds commenced spawning late in May and continued until September (Table 16).

It was concluded that oviposition on the shore continues from late April or early May to September, sometimes to early November. The maximum intensity of deposition occurs from May to July.

4. BEHAVIOUR OF FEMALE

Federighi (1931) established that *Urosalpinx* in America exhibits a negative geotaxis when the temperature rises above 10°C. In this country it seems to occur at about 7°C. This behaviour is particularly evident during the breeding season, when tingles adopt an elevated position to deposit their capsules. In the laboratory, it has been frequently observed that maximum spawning takes place near the water surface, even when adequate food is present on the tank bottom. In one experiment, a large number of tingles were placed in a big concrete tank with vertical sides. The depth of the water was 40 cm. and almost all the spawn was laid at the water surface. Two glass jars 20 cm. high were on the floor of the tank, and a number of groups of capsules were laid on those around the necks. When the water level was raised to 60 cm. many of the tingles moved up to the surface where some further spawn was deposited though the main spawning had been completed. This behaviour is also very noticeable in the field, where tingles choose their spawning sites above the bottom, and is of particular importance when planning trapping measures. It is associated also with the inshore movement of tingles during the breeding season. This movement has been studied by the use of marked tingles, examination of tile traps and dredging, and has been fully discussed in a previous section. Although this inshore movement does take place, a high proportion of the tingles lay their spawn below L.W.O.S.T. The spawn deposited on the shore has been shown to be only a fraction of the total quantity deposited. On the Common Shore in July, 1953, 79,000 capsules were removed in only four hours' dredging

Table 13: *Numbers of* Urosalpinx *capsules, full and hatched, collected in parallel dredge hauls over* 125 *m. with two* 4 *ft.* 6 *in. power dredges on the Southward Laying, River Crouch in* 1955. *Station* 1 *was* 10 *m. below L.W.O.S.T. and subsequent stations* 20 *m. apart.*

Station	*Date of collection*							
	23 *May*	29 *Jun.*	29 *Jul.*	26 *Aug.*	25 *Sep.*	27 *Oct.*	25 *Nov.*	*TOTAL*
1	19	957	1380	1091	106	55	41	3649
2	7	1232	1787	1439	338	52	3	4858
3	6	501	1596	311	78	31	60	2583
4	0	77	289	54	21	7	0	448
5	0	28	15	18	5	0	0	66
6	0	8	29	0	0	0	0	37
7	0	0	0	0	0	0	0	0
8	0	10	0	0	0	0	0	10
9	—	0	9	188	0	0	0	197
10		15	0	0	0	0	5	20
11		64	65	0	14	0	0	143
12		50	306	52	68	0	0	476
13		0	18	74	2	21	15	130
14		76	196	307	4	17	6	606
15		42	53	14	9	14	27	159
16		14	0	49	0	25	0	88
17		17	299	79	0	21	0	416
18		222	27	110	9	0	18	386
19		164	—	174	27	0	0	365+
20		298		104	5	0	0	407+
21		52		161	33	0	16	262+
22		23		51	0	0	—	74+
23		0*		—	0	—		0

*Base lines indicate end of stations sampled.

below L.W.O.S.T., whereas the greatest number of capsules taken from the shore of the same ground in one year on tiles and traps did not exceed 30,000.

During a dredge survey on the Common Shore in 1953, it was established that the maximum deposition of spawn occurred between 10 and 20 m. below L.W.O.S.T. (Fig. 3) at a depth of up to 1 m. Heavy spawning occurred from 0–40 m. offshore from L.W.O.S.T., and spawn was deposited at all depths in this part of the river, the maximum being 3½ m. On the Southward Laying, relatively little migration occurs on to the shore, and in 1955 most of the spawn was deposited between 20 and 40 m. below L.W.O.S.T., at depths of 0–2 m. (Fig. 5 and Table 13). Spawn has been taken at all stations across the river, the maximum depth here being 6½ m. Substantial numbers of capsules were taken in mid-river, associated with a submerged bank. Their presence is more likely to be the result of the more suitable substratum, than of the decrease in depth. In the intermediate zone of deeper water lies an almost pure culture of *Crepidula* and its shells (Table 15), with very little other life, and *Urosalpinx* and its spawn are only seldom found there.

5. CHOICE OF SPAWNING SITE

Carriker (1955) has suggested that the presence of suitable food material may influence the selection of the spawning site. On the Southward Laying, the proportion of tingles moving to the shore is small, and this could be due to the lack of food above L.W.O.S.T. At the Common Shore, large numbers of tingles move to the shore, where adequate food supplies, including oysters, are present. Roofing tiles used as traps (see p. 55) have proved ineffective unless 'weathered' by submerging them in sea-water for several months, due it is believed to the necessity for a covering of encrusting organisms.

Sizer (1936) reported that, in drill trapping experiments in Delaware Bay, the upper valve of a living oyster was preferred to the surface of an empty shell for oviposition.

Stauber (1943) found that traps baited with oysters attracted more oviposition than those containing shells. During some dredge surveys, the numbers of capsules and the objects on which they had been deposited were listed (Tables 14 and 15). The choice of object for oviposition reflects to a certain extent the substratum, since the maximum spawning occurs on these two grounds in the area of highest cultivation, carrying minimum numbers of *Crepidula*. On cultivated oyster bottom, shells, mainly from oysters, are predominant. On both the Common Shore in 1953 and the Southward Laying in 1955, it was found that the majority of spawn was deposited on oysters; on the Common Shore, there was less on medium-sized than on large oysters. Shell was the next favourite on both grounds, and on the Common Shore it was established that the inside of a pair of oyster shells or 'clock' was used much more often than the outer surface (Table 14). *Crepidula* was used much less frequently than either oysters or shell, but the insides of the empty terminal shells carried

Table 14: *Numbers of* Urosalpinx *capsules collected from specific spawning sites in parallel dredge hauls over* 100 *m. with two* 4 *ft.* 6 *in. power dredges on the Common Shore, River Roach on* 3 *June,* 19 *June,* 14 *July and* 27 *August,* 1953. *Station* 1 *was* 5 *m. below L.W.O.S.T. and subsequent stations* 10 *m. apart*

Spawning site	*Station*										
	1	2	3	4	5	6	7	8	9	10	*TOTAL*
Brood oyster .	1653	1674	949	409	186	224	46	103	46	30	5320
Adult oyster .	1748	1471	1014	1047	665	48	204	–	108	–	6305
Inside "clock" .	1189	990	887	766	244	–	11	–	33	–	4120
Outside "clock"	242	143	96	254	27	–	18	–	44	–	824
In *Crepidula** .	52	48	267	198	486	124	84	151	53	16	1479 } 1645
On *Crepidula* .	–	–	44	6	11	52	5	28	20	–	166 }
On shell . .	1129	675	276	–	7	–	25	85	16	46	2259
On *Ascidiella* .	–	–	152	–	–	–	–	–	–	–	152
On Stone .	7	–	–	–	–	–	–	–	–	–	7
On *Gryphaea* .	13	270	–	–	70	–	–	–	–	–	353

*'In *Crepidula*' refers to the inside of the terminal dead shell.

Table 15: *Numbers of* Urosalpinx *capsules collected from specific spawning sites in parallel dredge hauls over* 125 *m. with two* 4 *ft.* 6 *in. power dredges on the Southward Laying, River Crouch, on* 29 *July and* 26 *August,* 1955. *Station* 1 *was* 10 *m. below L.W.O.S.T. and subsequent stations* 20 *m. apart*

Station	*Spawning Site*				*Bottom*
	Oyster	*Shell*	Crepidula	*Stone*	
1	1781	684	6	–	Shell, Oysters, few *Crepidula*.
2	2747	467	12	–	Shell, Oysters, few *Crepidula*.
3	1636	264	7	–	Shell, Oysters, *Crepidula*.
4	250	3	90	–	Shell, *Crepidula*, few oysters.
5	9	–	24	–	Shell, *Crepidula*, oysters rare.
6	–	–	29	–	Shell, many *Crepidula*, oysters rare.
7	–	–	–	–	Shell, many *Crepidula*, oysters rare.
8	–	–	–	–	Shell, many *Crepidula*, oysters rare.
9	28	95	9	65	Shell, *Crepidula*, oysters rare.
10	–	–	–	–	Shell, *Crepidula*, oysters rare.
11	–	58	7	–	Shell, *Crepidula*, oysters rare.
12	230	108	20	–	*Sabellaria*, Shell, *Crepidula*, some oysters.
13	35	26	31	–	*Sabellaria*, Shell, *Crepidula*, some oysters.
14	327	106	10	60	*Sabellaria*, Shell, *Crepidula*, some oysters.
15	67	–	–	–	*Sabellaria*, Shell, *Crepidula*, some oysters.
16	37	–	–	12	*Sabellaria*, Shell, *Crepidula*, some oysters.
17	240	51	–	70	*Sabellaria*, Shell, *Crepidula*, some oysters.
18	57	9	25	46	*Sabellaria*, Shell, *Crepidula*, some oysters.
TOTAL	7444	1871	270	253	

nearly ten times as much spawn as the whole of the outer surface areas. Small quantities of spawn were found on *Ascidiella* and stones.

On the offshore part of Common Shore (Station 5—Table 14), where *Crepidula* is predominant, the few oysters present still carried the highest number of capsules. The selection of an elevated, yet shaded position, for spawning is evident from the choice of the inside of oyster 'clocks' or *Crepidula* shells, and is reflected in the way in which tingles nearly always spawn on the under-side of tile traps. Federighi (1931) and Cole (1942) showed that light has a limiting effect on the movement of tingles.

G. D. Waugh (personal communication) experimented in 1950 at the Common Shore with chicken-wire bag traps of the kind used in the U.S.A. (Stauber, 1938 and J. R. Nelson, 1931). 48 traps were used, baited with mussels, brood oysters, adult oysters and rocks, alternately, the line extending from 18 m. below to 29 m. above L.W.O.S.T. Analysis of Waugh's results has shown that in 1950, groups of spawn were deposited on the traps as follows: 457 on brood oysters, 443 on adult oysters, 318 on mussels and 86 on rocks. A study of the seasonal deposition of spawn on these traps (Fig. 20) gives further information on the summer migration of tingles during the spawning season (see p. 15).

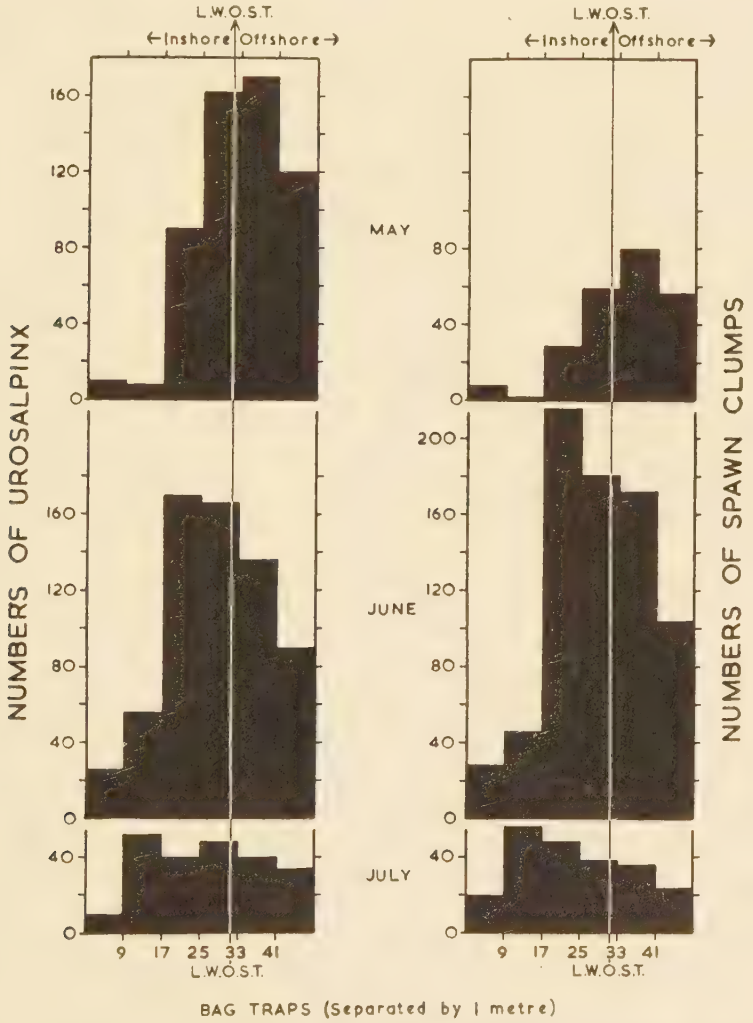


Fig. 20. *Numbers of* Urosalpinx *and clumps of its spawn collected from* 48 *wire bag traps placed at one-metre intervals, in a line extending from* 29 *m. above to* 18 *m. below L.W.O.S.T. at the Common Shore in May, June and July,* 1950; *the catches have been grouped at intervals of eight traps (from an experiment carried out by G. D. Waugh).*

6. GREGARIOUS BEHAVIOUR DURING OVIPOSITION

Cole (1942) observed that two or more drills are frequently found spawning together on the same shell with sometimes a dozen or more on a stone or pile of chain at low-water-mark, but believed this to be, not a social habit, but merely the close occupation of the available satisfactory spawning sites. Carriker (1955) observed similar behaviour in aquaria in the U.S.A., and felt that this was not the fundamental explanation. Observation of dredge catches over a period of years has shown that only a limited proportion of the numerous surfaces available carry spawn. At the height of the spawning season, a chosen object frequently bears 100 or more capsules, several times the total number estimated to be laid by one tingle. In June, 1953 one oyster was found to carry 606 capsules, this being one of only 9 spawning sites caught in two full hauls with 4 ft. 6 in. power dredges, containing oysters, shell and other material.

Inspections of tile traps used side by side at L.W.O.S.T. have shown that aggregations of tingles and spawn occur at intervals along the row. To a small extent, changes in the nature of the bottom may have an influence. In May, 1954, of 180 tingles taken from 50 tiles laid in a line over a very even shore, 49 were taken from one tile on which there was mass spawning. It is quite usual to find a series of tiles with no tingles or spawn, next to one or two tiles harbouring large numbers of both. In one laboratory feeding experiment in a porcelain sink 80×40 cm. containing numerous shells bearing oyster spat, 10 female tingles chose only 3 spawning sites; 5 tingles spawned together under one of the shells, 3 together on one side of the sink near the water level, and 2 others together lower down on another side. The first spawning occurred during the first week in May, and was followed by extensive movement, away from the spawn, for feeding. At the beginning of June, three of the tingles at least returned to their original spawning position, two under the shell, and one on the side of the sink, where each laid a small number of capsules. These observations imply a strong gregariousness in spawning behaviour, and it appears as though chemotaxis may play an important part. It is not suggested that the return of tingles to their own spawn is their usual behaviour, since obviously similar conditions were influencing their choice of spawning site on both occasions, and the tingles were artificially limited in their movement. It may, however, suggest that under confined conditions, tingles can not only detect the presence of other tingles or their spawn, but perhaps also even their own spawn. Federighi (1931) mentioned that in many cases the drill would return to its 'original' spawning position in the laboratory, but his observations showed that *Urosalpinx* spawned only once in a season unless disturbed, when it would cease, move away and recommence after a few days.

7. INCUBATION PERIOD AND HATCHING

Cole (1942), in the laboratory, observed periods of incubation of 27–32 days at an average temperature of 22·6°C. and 44–50 days at an average of 18·3°C., demonstrating the relationship between temperature and the duration of the incubation period. The slightly longer period of 7–8 weeks in the River Blackwater observed by him in 1941, was consistent with Orton and Lewis's (1931) records of temperature in that river, which varied from 13·5 to 19°C. between mid-May and August in the four years 1926–28 and 1930. Carriker (1955) has compared the observations of various workers in the U.S.A. with those from Britain, and it appears as though development in this country proceeds at a lower temperature than in the United States.

Observations for the Rivers Roach and Crouch are given in Table 9, and generally a period of 8–9 weeks elapsed before hatching. The average temperature over the first incubation period in 1953 was 15·9°C., several degrees lower than the average temperature of 18·3°C. at which Cole recorded an incubation period of 44–50 days. In the laboratory, 69 days incubation was observed in 1955, at an average temperature of 15°C. Certain figures in cols. 4 and 5 of Table 9 are only approximate, because observations were not made in the few days after the dates shown, when capsules had not begun hatching. This has been indicated by noting them as hatched 'after —', and the number of days as 'more

than —'. Some freshly deposited capsules taken from the Shop Laying on the 30th October, 1953 and placed in a laboratory aquarium had hatched by 5th January, 1954, after a period of 67 days. The mean temperature had fallen from 13° to 7°C. during this time, with an average of 10·5°C. There seems to be little difference between the incubation period at this temperature and that at 15°C. The influence of temperature is most apparent at 5°C. It was found (Hancock, 1956) that embryonic stages subsequent to the egg remained alive but dormant at this temperature, being able to continue their development when returned to water with normal summer temperatures after periods of several months. The lower temperature was shown to inhibit the loss of the operculum from the capsules at all stages of development. It was concluded that the loss of the operculum is brought about by dissolution of its cementing attachments by some enzyme which is released near to the time when gastrulation takes place. Its activity is inhibited by low temperature. It is unlikely that in normal hatching the operculum is released merely by bacterial activity, because, although it is released after a time similar to the normal hatching period in capsules with stages subsequent to the egg, it is retained for more than six months in capsules containing dead eggs. The incubation period is obviously closely related to temperature, but a more comprehensive series of observations is required before the exact relationship can be determined.

8. NUMBER OF CAPSULES

Since gregarious spawning is the rule, it is only by isolating one or a known number of females that the quantity of capsules deposited by one female can be found. In a laboratory tank in 1954, ten adult female tingles, kept throughout the year with some male tingles and fed with abundant oyster spat, were found to lay a total of 203 capsules. Of these, 162 were deposited between the 1st–10th May; a further 31 capsules were deposited between the 31st May–2nd June, at least three of the tingles taking part; 1 capsule was laid by another tingle on the 24th June, and a further 9 capsules by yet another between 9th–12th July. No spawning was observed after this date. All were mature females of 30 mm. length of shell or more. Cole (1942), by similar methods, found groups of 20 to 35 capsules laid in captivity, with an average of 25 per female. Carriker (1955), summarising the observations of various workers, showed that a much higher number of capsules had been recorded from isolated drills in America, the average per female varying from 28 (Federighi, 1931) to 57·6, with a maximum of 96 in Delaware Bay (Stauber, 1943).

In 1955, as previously mentioned, a two-year-old tingle in the laboratory deposited 9

Table 16: *Deposition of spawn by young tingles in the laboratory. Tank A contained three 2-year-old females, and Tank B, one 3-year-old and five 2-year-old females*

Date	*Tank A*		*Tank B*	
	Size range of tingles (mm.)	*Total number of capsules*	*Size range of tingles (mm.)*	*Total number of capsules*
6 Apr. 56 . .	15–17	–	14–18	9
11 May 56 . .	15–17	–	14–19	25
23 May 56 . .	15–17	5	14–19	39
20 Jun. 56 . .	17–19	19	15–22	68
16 Jul. 56 . .	18–21	35	18–24	87
7 Aug. 56 . .	19–21	73	18–25	119
29 Aug. 56 . .	21–23	104	19–26	147
25 Sep. 56 . .	22–24	114	20–26	147

small capsules only, late in the season. In the following year, it and five two-year-old females deposited 147 capsules between them, an average of 25. Three tingles hatched in October, 1954 commenced spawning on the 23rd May, 1956, and deposited 114 capsules, averaging 38 capsules. The deposition of spawn by these young tingles in the laboratory is shown in Table 16. The spawning period differs from that of older females in that it begins later, and is continuous. The capsules, at least at first, are small with a limited number of eggs. Cole (1942) found that three two-year-old tingles deposited small numbers of capsules, the most laid by one individual being thirteen.

9. SIZE OF CAPSULE

Pope (1910–11) recorded that drill egg cases in the Woods Hole area averaged 7 mm. in length and 4·5 mm. in width.

Observations on the size-distribution of *Urosalpinx* in the Rivers Roach and Crouch have shown that the modal and maximum sizes vary from place to place, even when separated by relatively short distances (Fig. 13). The lengths of capsules from the Southward Laying, the Common Shore and Paglesham Reach show a similar variation in

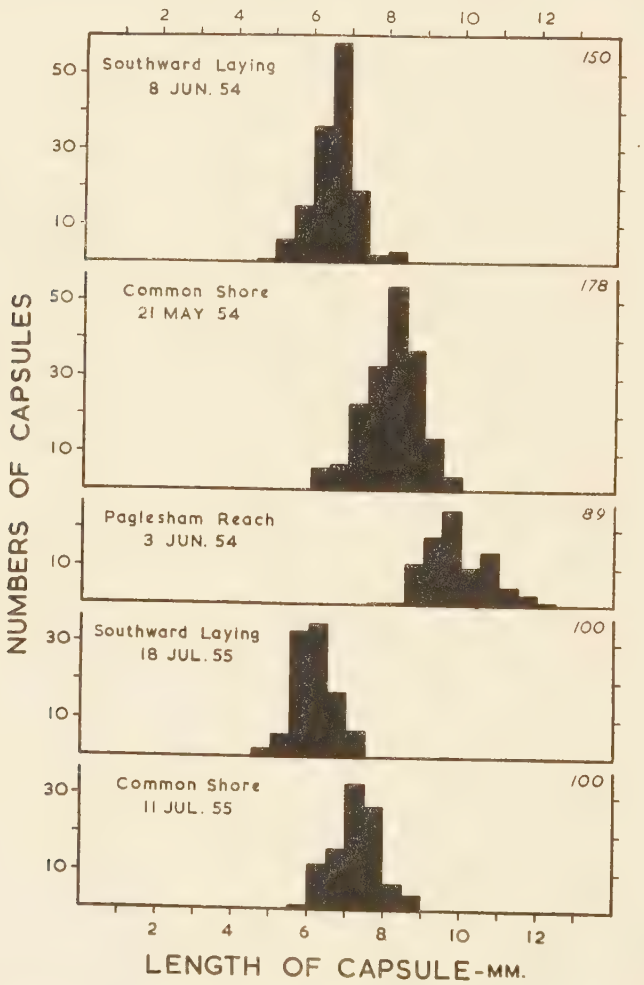


Fig. 21. *Size-distribution of* Urosalpinx *capsules from different localities. Capsule lengths have been grouped at 0·5-mm. intervals; the number in each sample is shown in the top right-hand corner.*

distribution. The size-distributions are compared in Fig. 21. The differences between the mean lengths for each locality are highly significant. The mean length of capsules from Paglesham Reach was over 3 mm. greater than that at the Southward Laying, but although younger tingles of similar size to those found at the Southward Laying are found at Paglesham Reach, none of the smaller sizes of capsules was taken there. This seems to imply an earlier maturity at the Southward Laying which has resulted in a smaller mean size of adults. The possible influence of diet has been discussed. Localised sampling seems to be important, since it appears that the largest capsules are associated with the largest tingles. The 9 capsules deposited in the laboratory by a two-year-old tingle of 26 mm. length at first maturity were all small, 5–6 mm. in length. In 1956, a nineteen-month-old, 17-mm. tingle deposited 5 capsules of 4-mm. length, and later 10 capsules of 5-mm. after it had grown by several millimetres.

10. NUMBER OF EGGS

Cole (1942) found that the number of embryos per capsule varied from 1 to 29, while the average number for 1423 capsules from different localities was 11·74 per capsule. Both the range and average number of eggs per capsule in England is greater than in the United States (Carriker, 1955), where the average number varies from 8 (T. C. Nelson, 1922) to 11 (Brooks, 1879–80). Observations in the Rivers Roach and Crouch show that the largest numbers of eggs per capsule are found in the largest capsules, which, in turn, are shown to be deposited by the largest tingles. In Fig. 22 the distributions of the numbers of eggs per capsule are compared for the Southward Laying, the Common Shore and Paglesham Reach. In samples of capsules, the mean numbers of eggs per capsule varied from 9·07 at the Southward Laying to 19·18 at Paglesham Reach (Table 17). By comparing Figs. 21 and 22, the close relationship between the length of the capsule and the number of eggs per capsule will be seen. The lengths of 977 capsules from different localities were measured and the number of eggs in each recorded. The results are shown in Fig. 23 and demon-

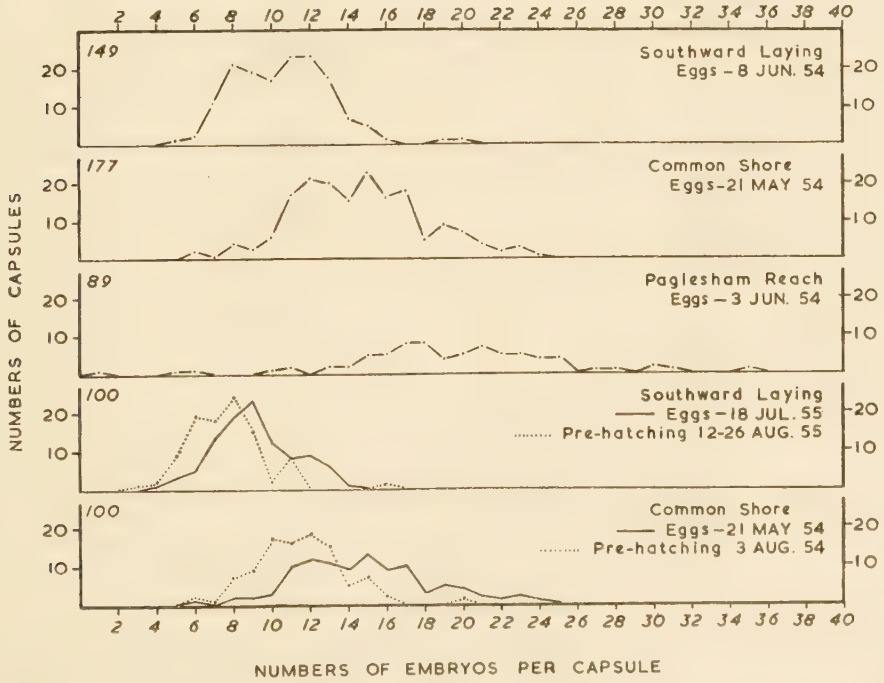


Fig. 22. *Distribution of numbers of embryos per capsule of* Urosalpinx *from different localities. The number in each sample is shown in the top left-hand corner.*

Table 17: *Average numbers of eggs per capsule and lengths of capsules from different localities in the Rivers Roach, Crouch and Blackwater*

Location	*Date*	*Stage*	*Number of capsules in sample*	*Mean number of eggs per capsule*	*Range*	*Mean length of capsule (mm.)*	*Range (mm.)*
Southward Laying, R. Crouch	11 Jun. 53	Egg	135	11·38	5–20		
	8 Jun. 54	Egg	150	10·59	5–20	6·48	4·8–8·2
		(small egg)		(0·25)	(0–4)		
	10 Sep. 54	Ready to hatch	48	9·29	3–14		
	6 Jul. 55	Egg	100	9·10	5–15	6·30	5·0–8·4
	18 Jul. 55	Egg	100	9·07	4–14	6·10	4·8–7·3
	12 & 26 Aug. 55	Ready to hatch	100	7·54	3–16	5·97	4·7–7·8
Common Shore, R. Roach	21 May 54	Egg	177	14·55	6–24	8·03	6·1–9·7
		(small egg)		(0·39)	(0–5)		
	3 Aug. 54	Ready to hatch	111	11·39	6–20		
	11 Jul. 55	Egg	100	12·19	7–27	7·25	5·7–8·9
	4 & 19 Aug. 55	Ready to hatch	92	10·05	4–15	7·10	5·0–9·0
West Mersea R. Blackwater	10 Jun. 55	Egg	108	10·90	0–17	7·42	5·7–9·2
Creeksea Laying, R. Crouch	24 Jun. 54	Egg	100	13·14	0–34	7·57	6·0–9·2
Paglesham Reach, R. Roach	3 Jun. 54	Egg	89	19·18	5–35	9·80	7·7–12·3
		(small egg)		(0·55)	(0–5)		

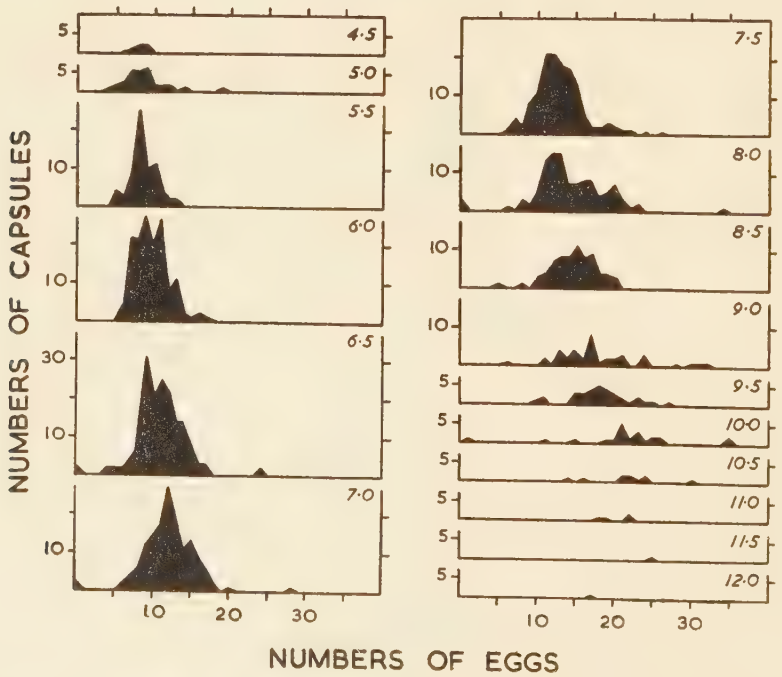


Fig. 23. *Relationship between capsule length and distribution of numbers of eggs per capsule in* 977 *capsules of* Urosalpinx *from the Rivers Roach and Crouch. Capsules have been grouped according to length and are shown separately at intervals of* 0·5 *mm. The length in mm. of each group of capsules is shown in each top right-hand corner.*

strate quite clearly the proportional relationship between the size of the capsule and the number of eggs. The largest number of eggs found in one capsule from normal samples was 35 at Paglesham Reach, but on the 7th July, 1955, a 6-mm. capsule containing 72 eggs, an 8-mm. capsule containing 89 eggs, and a 6-mm. capsule with 273 eggs were all taken at the Common Shore. Reference to Fig. 23 will confirm that these are most unusual. Capsules containing no eggs also occur, but were found only seven times in the sample of 977 capsules used for Fig. 23. Carriker (1955) reported that Stauber (1943) found, in general, that the largest drills laid larger egg cases which in turn contained more ova than the capsules of small drills. This is evidently the case, and these observations assume importance when sampling, not only because of the differences in population between localities, but because of seasonal changes in the spawning population. It has been shown that the older females spawn earlier in the season, and are followed later on by females predominantly smaller and younger. Females at first maturity seem to deposit a few relatively small capsules towards the end of the season. It is therefore to be expected that the mean size of the capsule and, more important, the number of eggs, will fall throughout the season. Measurements made were not planned with this in view, so that no series of results from the same year is available for comparison. However, from Table 17 it can be seen that there is a tendency for capsules deposited early in the season (May-June) to be larger and to contain more eggs than later ones (see also Figs. 21 and 22). This should be considered when comparing the intensity of oviposition in different localities, and also when comparing samples taken from one locality in order to estimate the mortality during development. For example, to estimate the mortality in capsules by comparing samples deposited in May with a sample containing juveniles in September might be quite misleading.

There appears to be some variation in capsules from one parent. A 17 mm. female deposited five 4-mm. capsules containing 5–7 eggs, and later, after it had grown by a few millimetres, ten 5-mm. capsules containing 6–8 eggs. A young isolated 26-mm. female *Urosalpinx* laid nine small (5–6 mm.) capsules in which the number of eggs varied from 8 to 12. Small groups of capsules taken from the Southward Laying in 1953, each group probably being deposited by one parent, were examined and considerable variation in the number of eggs per capsule was found. The distribution of the numbers of eggs per capsule in representative groups is shown in Table 18. A study of the capsules of *Ocenebra* and *Buccinum* has also shown that there is some variation in both the size of the capsules and the number of eggs they contain, from one parent.

Table 18: *Distribution of number of eggs per capsule in selected groups taken from the Southward Laying in* 1953

Number of eggs per capsule	*Group*								
	I	*II*	*III*	*IV*	*V*	*VI*	*VII*	*VIII*	*IX*
0	1	–	–	–	–	–	–	–	–
6	–	–	1	–	–	–	–	1	1
7	–	1	3	1	–	–	–	1	6
8	1	–	2	1	3	1	5	3	5
9	1	2	1	–	5	–	2	5	3
10	4	6	4	3	2	–	1	5	5
11	1	4	2	4	4	1	–	5	2
12	–	2	4	5	–	3	–	4	3
13	1	1	1	3	1	1	–	2	2
14	2	–	2	2	–	2	2	1	2
15	1	–	–	2	–	–	5	–	–
16	1	–	–	2	–	–	–	–	1
17	–	–	–	1	–	–	–	–	–
18	–	–	–	2	–	–	–	–	–
19	–	–	–	–	–	–	–	–	1
20	–	–	–	1	–	1	–	–	–
Total capsules in group	13	16	20	27	15	9	15	27	31

11. NUMBER HATCHING

Cole (1942) found an average of 12·47 early stages per capsule and 10·74 shelled stages, indicating a mortality during incubation of 1·73 embryos per capsule or 13·9%. These capsules, totalling 1423, were taken from different localities. The importance of care in sampling, particularly in this instance, has been mentioned previously. Limited comparisons have been made using small samples of about 100 capsules made up of lots of no more than two capsules from any group of spawn, in order to minimise influence from one parent. At the Southward Laying the difference between the mean number of eggs per capsule on the 18th July, 1955 and the mean number of juveniles per capsule in August was $1{\cdot}53 \pm 0{\cdot}29$, or a mortality of 16·9%, and between Common Shore samples for 21st May and 3rd August, 1954 was $3{\cdot}16 \pm 0{\cdot}34$, or 21·7% mortality (Fig. 22 and Table 17).

The observations of Federighi (1931) show that mortalities of up to 42% may occur in America. Brooks (1879–80) first showed that abnormal eggs are frequently found in egg capsules, and that occasionally an advanced embryo breaks up and these swimming fragments are consumed by other embryos. Haskin (1935) observed some atypical spermatozoa in gonad smears of *Urosalpinx*, and suggested that they may be responsible for the fertilisation of eggs which produce abnormal embryos. A few very much smaller eggs occur frequently among normal eggs, and undefined pieces of yolk material are not unusual. The number of these smaller eggs seems to increase with the number of normal eggs. The average number of smaller eggs per capsule was found to be 0·25 at the Southward Laying, 0·39 at the Common Shore, and 0·55 at Paglesham Reach. The disappearance of these smaller eggs by no means accounts for the total mortality. Rather, it appears that they give rise to the retarded veligers which are frequently seen, and which are probably devoured by the more advanced normal stages.

VIII. RELATION TO ENVIRONMENT

1. TEMPERATURE

The activities of *Urosalpinx* seem to be greatly dependent on temperature conditions. During the winter months, tingles in the field and laboratory are found in a hibernating condition, the former sometimes occurring many metres above L.W.O.S.T., with only the tips of the siphons protruding from the mud, occasionally under rocks, and always with the foot attached to a small piece of shell or stone under the surface of the mud. Tingles kept in an outdoor tank were found to be still attached to the glass bottom of the tank at a temperature of $-0{\cdot}5$°C., when ice had formed on the surface. On one occasion in the laboratory, a tingle was observed in the process of burying itself in a mud and shell bottom. It first made a series of semicircular movements to and fro and the lip of the shell made a substantial depression in the mud. It then moved forward a little and the top of the spire tilted back and downwards into the depression where it remained. Possibly further covering takes place by silting. Laboratory observations showed that hibernation commences and ends at a temperature of about 7°C. Occasional movements were observed below this temperature, and some tingles remained quiescent even when the temperature had risen to 10°C. Feeding commenced at 9–10°C., and deposition of spawn at 11–12°C. These temperatures have been found to be consistent for *Urosalpinx* from the Rivers Roach and Crouch, and represent the minimum temperatures at which the particular activities have been observed. Presumably, natural variations in the responses by individuals will occur as with all other processes. Investigators have shown that in many instances, the minimum thermal limits, above which these physiological functions occur, decrease progressively northwards in the latitudinal distribution of the species (Carriker, 1955).

Orton and Lewis (1931) showed that although numbers of *Nucella* were severely reduced, and *Ocenebra* suffered virtual extinction, *Urosalpinx* was unaffected by the severe winter of 1929 when temperatures in the River Blackwater fell to −1·5°C. and sub-normal temperatures were sustained during the winter. Cole (1942) found that following the very cold winters of 1939–40 and 1940–41, *Ocenebra*, which had been slowly increasing, was represented only by dead shells, though no significant change in the numbers of dead shells of *Urosalpinx* had occurred. In the Rivers Roach and Crouch in 1954, sub-zero temperatures lasted for nearly two weeks, falling to −1·9 C., and in 1955, for over five weeks, falling to 2·0 C., with no apparent harm to the *Urosalpinx* population. It has been shown (Hancock, 1956) that *Urosalpinx* capsules deposited late in the year could survive these winters in a state of inhibited development, provided embryos had reached the stage of gastrulation, to continue their development in the following spring. Egg stages were killed in the laboratory at 5°C.

2. SALINITY

Researches on salinity in the United States showed conclusively that the variables of temperature and time exert a significant influence on rate of survival: at optimum summer temperatures, the mortality rate of drills increases rapidly as salinities fall, but this rate is markedly reduced as temperatures drop, so that at low winter temperatures *Urosalpinx* can withstand unusually low salinities for protracted periods (Carriker, 1955). The conditions in the Essex estuaries are such that only the narrow headwaters undergo marked changes in salinity, and populations of *Urosalpinx* there are rarely large enough to show clear evidence of appreciable mortality. At Fambridge, River Crouch, the population of tingles is small, and the lowest winter salinities recorded were 21·7‰ in December, 1952, 15·3‰ in February, 1954 and 18·5‰ in February, 1955. Adult *Urosalpinx* and spawn were taken higher up than Fambridge in Brandy Hole, River Crouch during 1955. Stauber (1943 *cit.* Carriker, 1955) concluded that at low winter temperatures *Urosalpinx* can survive for lengthy periods in salinities as low as 8‰.

3. CURRENT, LIGHT, GRAVITY

Federighi (1931) showed that a *Urosalpinx* placed in a water current will immediately orientate itself with the siphon pointing upstream and move against the current. This is often seen in laboratory tanks, when the tingles are found to congregate around the inflow pipe, and if it is accessible and wide enough, may crawl up inside it against the current. Federighi (1931) demonstrated that *Urosalpinx* exhibits a negative geotaxis at summer temperatures, but was not sure of the explanation for the absence of any negative geotaxis during the winter months, when hibernation just below the surface takes place. The use of marked tingles at the Common Shore, showed that the direction of migration on the shore depended (a) on the time of the year and (b) on the position on the shore at which they were released. Tingles released high on the shore moved down the shore, whether liberated in June or September. This behaviour, and the manner in which tingles move from the walls of laboratory tanks to the hibernating position on the bottom, suggests a reversal rather than an absence of a negative geotaxis. The movement of tingles downshore at summer temperatures implies that temperature is not the only factor responsible for this change in behaviour, unless with longer periods of exposure, higher air temperatures cause a similar tactic reversal. It could equally well have been associated with the influence of extended exposure in strong sunlight. Sizer (1936) and Cole (1942) have both observed that tingles show a negative response to all but low intensities of sunlight, moving where possible into the shade.

4. EXPOSURE

The survival of *Urosalpinx* after exposure to air at different temperatures was examined by leaving a large number of tingles on an enamel tray, recording maximum and minimum temperatures, and returning a number (usually ten) to sea-water at intervals. The results (Table 19) are not conclusive, but it is evident that there is greater survival at lower air temperatures. The air temperature had a much greater daily range than their normal

Table 19: *Survival of* Urosalpinx *after exposure to air at different temperatures—a group of tingles was returned to sea-water after each exposure period*

Date experiment commenced	*Temperature (°C.)*		*Period of exposure*	*Survival*	*Number used for each exposure*
	Min.	*Max.*			
7 Mar. 55	—3	9½	5 days	Yes	2–3
			7 days	Yes	
			8 days	Yes	
			9 days	Alive, but very slow to recover	
			10 days	Alive, but did not recover	
			11 days	Did not recover	
18 Mar. 54	4½	18	Up to 5 days	100%	10
			6 days	60%	
			7 days	30%	
			8 days	20%	
			9 days	0%	
27 Oct. 53	11½	17	42 hrs.	100%	10
			66 hrs.	100%	
			90 hrs.	70%	
			136 hrs.	0%	
			151 hrs.	0%	
1 Jul. 53	18½	29	24 hrs.	100%	20
			48 hrs.	45%	
			72 hrs.	5%	
			96 hrs.	0%	
			120 hrs.	0%	

environment. At low temperatures *Urosalpinx* can survive at least 8 days' exposure to air, compared with only 3–4 days at higher temperatures. These figures were obtained under dry conditions; no doubt in the very damp, cool conditions used for transport of oysters, *Urosalpinx* could survive for much longer periods. Capsules exposed for 26 hours continued development when returned to sea-water. Presumably, humidity and wind would influence survival.

5. OTHER ANIMALS

As with most shelled animals, the shell of *Urosalpinx* provides a home for *Polydora*, bryozoans and other encrusting organisms.

Various American authors have observed that starfish will feed on oyster drills, and were in agreement that *Asterias forbesi* devours *U. cinerea* but only when oysters and other bivalves are not obtainable. It was shown (Hancock, 1955) that in Britain *Asterias rubens* will eat *Urosalpinx* even in the presence of oysters, oyster spat and many other species of shellfish. *Asterias* confined with equal numbers of oysters, oyster spat, *Crepidula* and *Urosalpinx*, ate mostly *Crepidula*, but significantly more *Urosalpinx* than oysters or oyster spat.

IX. CONTROL

THE importance of *Urosalpinx* as a pest of oyster culture has been established, and it was concluded (Hancock, 1954) that the large-scale removal and destruction of *Urosalpinx* would, under existing biological relationships in Essex rivers, allow increased survival of oyster spat and oysters. Efforts to devise control measures have included a study of the relation of *Urosalpinx* to existing methods of cultivation, experiments with mechanical methods of capture, and studies on the biology and habits of *Urosalpinx* as a means of developing methods of trapping and destroying them.

1. PRESENT METHODS OF OYSTER CULTIVATION

The normal methods of dredging with and without the use of power in Essex rivers have been described in detail by Cole (1956). Although, during normal dredging, tingles are rigorously removed and destroyed, the dredge is an inefficient way of clearing the bottom, particularly of *Urosalpinx*. Waugh (personal communication) established without doubt that dredges fitted with 'brood rigging', i.e. a belly constructed with rings of 1-inch diameter, are more efficient than dredges with normal rigging of 1½-inch diameter mesh, the relative catches of tingles being in the ratio of 13 : 10. This method of control could be of only limited application, because on areas with a high proportion of small shells, the dredges fill too quickly and catches of oysters are reduced. Cole (1942) found that on muddy ground, washing of the dredge to the extent necessary to free it from mud resulted in the loss of 75–100% of the tingles, and advocated washing the catch by buckets on deck.

An estimate of the efficiency of the power dredges carried by the Ministry's research vessel WYSTRYS when used for catching tingles can be obtained from Fig. 4 which shows the catches by two 4 ft. 6 in. dredges over 125 m. on each station at the Southward Laying. The greatest number taken during 1955 in one haul with two dredges was 74 on Station 1 on the 26th August. The population density estimated by grab survey on Station 1 was 7–8 tingles per sq. m. The area covered by the dredges was roughly 350 sq. m., giving an efficiency of about 3%. This was the maximum efficiency observed during the season, and when Fig. 4 is compared with the numbers from the grab-survey (Fig. 6) it is clearly seen that the dredges are much less efficient in retaining tingles throughout the rest of the year.

At the Common Shore, yields of 18 and 24 tingles per haul with two 4 ft. 6 in. dredges over 100 m. were obtained on the 27th August, 1953 compared with catches of 4–5 per sq. m. from the grab survey a few days previously. This represents an efficiency of only 2% for the dredge. Higher catches were obtained from this ground on the 19th June during the onshore migration (Fig. 3).

It has been shown that *Urosalpinx* hibernates beneath the surface of the mud in winter and at this time is less likely to be caught in the dredge. In spring, as the temperature rises, there is increasing activity accompanied by the elevation of *Urosalpinx* on to larger objects, particularly oysters. The movement is associated with feeding and breeding and at this time they cling more firmly to their substratum and are then more likely to be retained in the dredges. It can be seen from Figs. 3 and 4 that the largest numbers of tingles are dredged during June and July. Female tingles captured in April and May are of greater relative value because they will have been prevented from laying their spawn.

The area which should be dredged most intensively varies in different localities, but can readily be ascertained by a series of parallel dredge hauls (Figs. 3 and 4). At the Southward Laying it extends to 60 m., and, at the Common Shore, to 40 m. offshore from L.W.O.S.T. Thus although normal dredging is not very efficient for capturing tingles, it can be used to maximum advantage by selecting the right time and place. The survival of tingles after

exposure to air for up to 8 days has been demonstrated (p. 50). Dredged tingles should, therefore, not be returned until after adequate drying.

An examination of the spawn taken in dredge hauls shows the great use which can be made of dredging at the right season. The maximum number of capsules taken in one haul with two 4 ft. 6 in. power dredges at the Southward Laying was nearly 1800 on the 29th July, representing about 16,000 hatching juveniles (Fig. 5); on the Common Shore, nearly 2,500 capsules were taken in one haul on Station 2 on the 19th June (Fig. 3). From Fig. 19 it can be seen that June, July and perhaps August are the best months for dredging for spawn; of these months June is likely to be the most profitable since few juveniles will have hatched. Four hours dredging at the Common Shore with two power dredges on the 22nd July, 1953 yielded 250 tingles (including 146 females) together with 79,000 capsules of spawn. This represented the spawn deposited by some 3,000 tingles, and the destruction of about 790,000 juveniles. The normal power dredge is, therefore, a most efficient way of capturing the spawn of *Urosalpinx*, and this efficiency may be maintained by a knowledge of when and where to use it.

It can be seen from Table 8 that although the larger proportion of tingles taken during the summer months are females, the reverse is often the case in winter. This difference is ascribed to differential sexual behaviour in and out of the breeding season. The size-distribution of *Urosalpinx* collected in dredges always shows a higher proportion of larger sizes than those collected by other means, due to the loss of smaller tingles through the rings. Since the male *Urosalpinx* has consistently been shown to have a smaller size-range than the female, this would contribute to the larger proportion of females taken in dredges. Cole (1942) felt that the loss of young tingles up to three years old was not a serious matter in view of the limited amount of spawn deposited by them. They are known, however, to do serious damage to small spat. The fact that they would not be captured until mature, decreases the chances of complete control by mechanical means, because each time the adult population has been reduced to a less dangerous level, replacement from the lower year-groups will take place. Smaller tingles are also only poorly represented in catches on traps.

2. TINGLE DREDGES

According to Carriker (1955) the first tingle dredge was invented in the late 19th century (Moore, 1898). A wedge-shaped dredge was fitted at the top with an inclined perforated screen, and when dragged over oyster beds, the oysters were forced over the dredge and tingles fell into the dredge pan. Federighi (1931) and Galtsoff *et al.* (1937) have drawn and described two tingle-dredges based on this principle. J. R. Nelson (1931) used three types of tingle dredge, but concluded that oysters were damaged, the dredge choked with dirt and the catch of tingles was not worth while.

Tingle dredges after the pattern of the one described by Galtsoff *et al.* (1937) have been constructed and used in this country. Instead of one-inch-square mesh network for the inclined screen, the ring rigging used in normal dredges was employed. It was believed that this would cause greater vibration of material passing over the screen, and consequent detachment of the tingles, which would fall into the pan. Tingle dredges of this type, suitable for operation by hand as well as by power, have been compared extensively with normal dredges but the best catches made by the tingle dredges only equalled those of the power dredges. The latter were effective in retaining, in addition, oysters and large quantities of tingle spawn. During the winter, when the number of tingles caught by power dredges was severely reduced, even fewer were taken by tingle dredges. The main advantage of such tingle dredges could lie in the fact that the catch need not be sorted, but merely emptied and bagged up for drying ashore. In Essex, however, the work involved in moving the enormous volume of small shell retained by the dredges is not warranted by the number of tingles captured. It seems likely that tingle dredges can have only limited application in this country. Work is being continued on a smaller type, which could be attached to a hand-dredge frame, and would require lifting only after several tows of the normal dredges.

3. TRAPS

Bags made of galvanized chicken-wire, filled with oysters as bait and attached to lines, have been used successfully in the United States. Galtsoff *et al.* (1937) have described the refinements of methods of using bag-traps and the bait required. Stauber and Lehmuth (1937) calculated that this method of trapping could be used economically, and decided that there was no other method as efficient for catching tingles during the first season when seed oysters were laid on a ground. There has, however, been no widespread adoption of this method of controlling the oyster drill (Carriker, 1955). Experiments with similar traps in this country have met with little success. G. D. Waugh (personal communication) has used them at the Common Shore both above and below low-water-mark, and the author has tried them at the Southward Laying. The small number of tingles taken by no means justified the time and difficulty involved in inspecting the traps; this result may have been a consequence of the distribution of *Urosalpinx* below low-water-mark, which is usually related to the greatest densities of food, so that the traps would provide little attraction except perhaps as spawning sites. Dredging is, however, a far more efficient way of collecting spawn.

Cole (1942) felt that the detachment of men from normal dredging operations for the work of hand-picking on beaches was justified in the River Blackwater. T. C. Nelson (*cit.* Carriker, 1955) suggested that damage to oysters by the feet of oystermen might equal that caused by the tingles removed, and that careful hand-picking would involve turning over every oyster and shell which might permit tingles to lodge underneath.

The foregoing studies on the behaviour of *Urosalpinx* have established (1) a movement into the intertidal zone during the summer, (2) the need for an elevated but shaded position

Table 20: *Numbers of* Urosalpinx *collected from tile traps at the Common Shore, River Roach, in* 1953 *and* 1954. *The positions of the rows are shown in Fig.* 7—*each row contained* 50 *tiles.*

Date	*Row*				
	A	*B*	*C*	*D*	*M*
14 Jul. 53 . .	2	15	2	10	40
12 Aug. 53 . .	7	5	22	5	45
27 Aug. 53 . .	15	9	20	11	42
15 Sep. 53 . .	28	39	77	14	46
29 Sep. 53 . .	70	41	83	32	35
13 Oct. 53 . .	*NE	33	*NE	33	15
27 Oct. 53 . .	30	41	77	15	21
9 Nov. 53 . .	9	11	21	2	10
26 Nov. 53 . .	4	1	5	2	7
11 Dec. 53 . .	3	0	4	1	5
TOTAL . . .	168	195	311	125	266
5 May 54 . .	25	24	34	17	17
21 May 54 . .	89	64	175	68	58
3 Jun. 54 . .	99	112	185	224	44
18 Jun. 54 . .	84	80	157	177	29
2 Jul. 54 . .	57	76	87	111	18
19 Jul. 54 . .	49	62	113	79	21
3 Aug. 54 . .	49	31	77	58	23
17 Aug. 54 . .	19	30	59	40	15
31 Aug. 54 . .	10	20	35	34	19
15 Sep. 54 . .	12	20	39	33	11
29 Sep. 54 . .	8	20	34	32	17
15 Oct. 54 . .	8	25	27	30	15
1 Nov. 54 . .	8	24	9	12	26
15 Nov. 54 . .	2	4	8	3	5
TOTAL . . .	519	592	1039	918	318

*NE = Not examined.

for the deposition of spawn and (3) a gregarious behaviour during spawning. The ideal trap is one which embodies these three properties. Curved roof tiles have been used with success along the shore at L.W.O.S.T. Each measures 19×6 in., and they are placed in a row with the convex side uppermost.

On the 1st July, 1953 rows of tiles were placed at the Common Shore, River Roach as in Fig. 7. Rows A–D and M were each composed of 50 tiles, side by side in a straight line, with long axes parallel to the water's edge. Rows A–D were tiles just taken from land, while those in Row M had been in the intertidal zone for more than a year. All these tiles

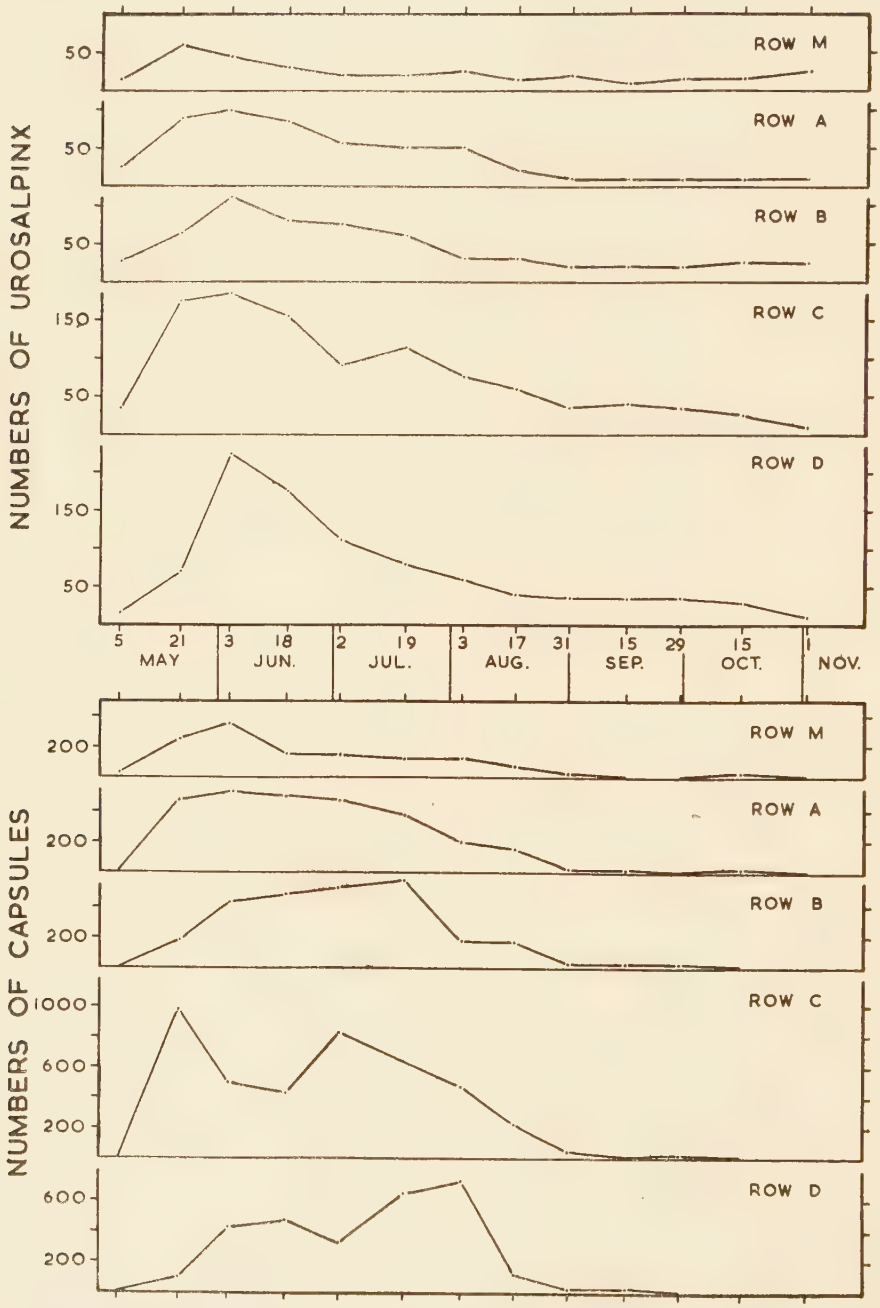


Fig. 24. *Numbers of* Urosalpinx *and its capsules collected from rows of tile traps at the Common Shore, River Roach, in* 1954. *Each row contained* 50 *tiles.*

were left in position throughout 1954 and 1955. The results for 1953 and 1954 are shown in Table 20, and it can be seen that in 1953 the best catches were obtained from Row M. In the next year, Row M was found to be the least efficient, due to being screened from migrating tingles by Row A. The initial success of Row M was due to the fact that the tiles had undergone a period of exposure to sea-water; in consequence, fouling organisms had settled and they resembled a piece of natural shore. Initial failure of tiles to trap tingles has been experienced on several occasions, again due to the newness of the tiles. Results on the Common Shore in 1954 (Fig. 24) show that tingles and spawn, in numbers, appeared first on the rows lower down the shore (A to C) and subsequently on those 5 m. above (B and D).

Tiles placed 30 m. and 45 m. above L.W.O.S.T. (Rows R and S, Fig. 7) captured 317 and 68 tingles on 180 and 30 tiles respectively in 1954 despite the screening action of tiles of rows Q and P near L.W.O.S.T. These catches show the extent to which tingles move up the shore, but are insignificant when compared with catches from Rows A–D. Row P at L.W.O.S.T. was, in 1954, composed of one series of tiles placed side by side, and another series separated by gaps. Throughout the year the separated tiles caught more than those placed together, in the ratio of 7 : 3.

Table 21: *Numbers of* Urosalpinx *captured on tile rows E–K at L.W.O.S.T. at the Common Shore, River Roach, 22 June–5 October,* 1955

Row	*No. of tiles*	*Spacing*	*Relation of long axis of tile to water's edge*	*No. of tingles caught*	*Changed efficiency per tile*	*Changed efficiency per distance*
E	25	Together	Parallel	99	–	–
F	25	2 tile-lengths apart	Parallel	176	× 1·9	× 0·6
G	25	Together	Parallel	88	–	–
H	25	1 tile-length apart	Parallel	89	× 1·1	× 0·5
I	25	Together	Parallel	74	–	–
J	25	Fairly close	Perpendicular	157	× 1	× 1
K	25	Together	Parallel	240	–	–

Table 22: *Numbers of* Urosalpinx *and their capsules captured on tile rows I–VII at L.W.O.S.T. at the Shop Laying, River Roach,* 24 *May–5 October,* 1955

Row	*No. of tiles*	*Spacing*	*Relation of long axis of tile to water's edge*	*No. of tingles caught*	*Changed efficiency per tile*	*Changed efficiency per distance*	*No. of capsules caught*
I	25	Together	Parallel	122	–	–	1,105
II	50	Fairly close	Perpendicular	286	× 0·7	× 0·7	1,893
III	25	Together	Parallel	298	–	–	1,917
IV	25	1 tile-length apart	Parallel	359	× 1·0	× 0·5	3,373
V	25	Together	Parallel	387	–	–	4,008
VI	25	4 tile-lengths apart	Parallel	992	× 2·7	× 0·5	13,911
VII	50	Together	Parallel	700	–	–	7,371

Table 23: *Numbers of* Urosalpinx *and their capsules captured on tile rows* 1–7 *at the Shop Laying, River Roach,* 14 *May–*8 *October,* 1956 (*all tiles parallel to the water's edge*)

Row	*No. of tiles*	*Spacing*	*No. of tingles caught*	*Changed efficiency per tile*	*Changed efficiency per distance*	*No. of capsules caught*
1	25	Together	133	–	–	612
2	25	2 tile-lengths apart	308	× 1·5	× 0·5	2,670
3	25	Together	276	–	–	1,140
4	25	3 tile-lengths apart	866	× 2·3	× 0·6	5,085
5	25	Together	487	–	–	2,093
6	25	4 tile-lengths apart	1087	× 2·0	× 0·4	11,132
7	25	Together	643	–	–	5,065

To determine the most efficient placing of tiles, a long row of tiles at L.W.O.S.T. on the Common Shore was divided up in 1955 as in Fig. 7 and Table 21. A similar row was divided up at the Shop Laying in 1955 and 1956 (Tables 22 and 23). Each set of separated tiles was usually placed between two rows of 25 tiles laid side by side and parallel to the water's edge. The catches of the separated tiles were then compared with the average of the catches of the rows on each side to calculate (see (1) below) the changed efficiency due to separating the tiles. In this way errors due to uneven distribution of the population were minimized. The catching efficiency of the tiles, when related to the distance of shore covered, was also changed by separating the tiles. This change (see (2) below) was estimated by comparing the number caught by the row of separated tiles, with the expected catch if the same distance had been covered by tiles placed side by side. The expected catch was again calculated from the average numbers caught by adjacent rows of unseparated tiles. Tables 21–23 show the results obtained. A typical calculation was as follows:—

Row F—Common Shore, 1955: *Tiles placed two tile-lengths apart.*

Number captured on Row F = 176 or 7·0 per tile.

Number from 25 tiles placed side by side = Rows $\frac{E + G}{2} = \frac{99 + 88}{2} = 93{\cdot}5$ or 3·7 per tile.

(1) ∴ Efficiency per tile of separated tiles has been increased in the ratio $\frac{7{\cdot}0}{3{\cdot}7} = \times 1{\cdot}9$.

(2) Catching efficiency per tile when related to the distance of shore covered by the row, has been decreased in the ratio $\frac{7{\cdot}0}{3{\cdot}7 \times 3} = \times 0{\cdot}6$.

From Tables 21–23 it can be seen that largest catches per tile came from those separated by gaps of 4 tile-lengths, when the expected catch was multiplied by more than two. However, this row only caught about half the number expected if the same distance had been covered by tiles side by side. Such a row would, however, have involved the use of five times the number of tiles and taken longer to inspect. The use of tiles would best be based on the number of tiles and the time available. On a long stretch of shore, separated tiles would give the overall benefit of trapping larger numbers, whereas tiles concentrated over a shorter distance, though catching less, would show more obvious signs of reducing the population. Figures for spawn caught at the Common Shore in 1955 are not shown, because they were influenced by the spawning of marked and liberated tingles. The spawn collected from Shop Laying tiles (Tables 22 and 23) showed that the efficiency per tile of those placed 4 tile-lengths apart was increased 3·6 times in 1955, and 3·1 times in 1956. This was due to the gregarious behaviour of *Urosalpinx* during spawning. Tiles placed with axes at

right-angles to the water's edge were generally much less efficient, due largely to the accumulation of silt in the eddies formed under the tiles.

The shores at the Shop Laying and the Common Shore slope gradually and are composed of mud made firm by small shells, with no shortage of the tingles' natural food. At the Southward Laying, however, tiles have been used for three years with little success, for there, although the population density is larger, the proportion moving on to the shore in summer is much smaller. The shore is somewhat steeper than the Common Shore, there are some patches of soft mud, and food is scarce. The number of tingles and spawn taken from a long row of boulders, the 'stone hedge', marking L.W.O.S.T. seldom warranted the time spent inspecting them. It is hoped that traps constantly submerged below low-water-mark will prove more successful.

Lines carrying modified tile traps have been used underwater with some success. On the 24th May, 1955, at the Common Shore, eleven traps, each made of 4 ordinary tiles wired into two tiers or 'bouquets', were attached to a rope line 5 m. below L.W.O.S.T. (the lower pair of tiles ensures that the top ones are sufficiently elevated from the mud). The bouquets had been previously 'weathered', and they caught 554 tingles and 289 capsules during 1955. This equalled the catches made by some of the rows of 50 tiles at L.W.O.S.T. Larger ridge tiles (12×11 in.) wired individually to the same line, were quite successful, but they were new when put down in 1955. In 1956 at the Common Shore, 14 bouquets captured 431 tingles and 3,151 capsules, and 24 large tiles captured 563 tingles and 3,363 capsules. These catches per trap were only bettered that year by the two highest catches per tile (Rows 4 and 6 at the Shop Laying, Table 23).

4. EFFECTS OF TRAPPING

In 1953, the grab survey showed that at the Common Shore there were about 32,000 tingles on the whole oyster laying. In the years 1953–1955, nearly 23,000 tingles and countless

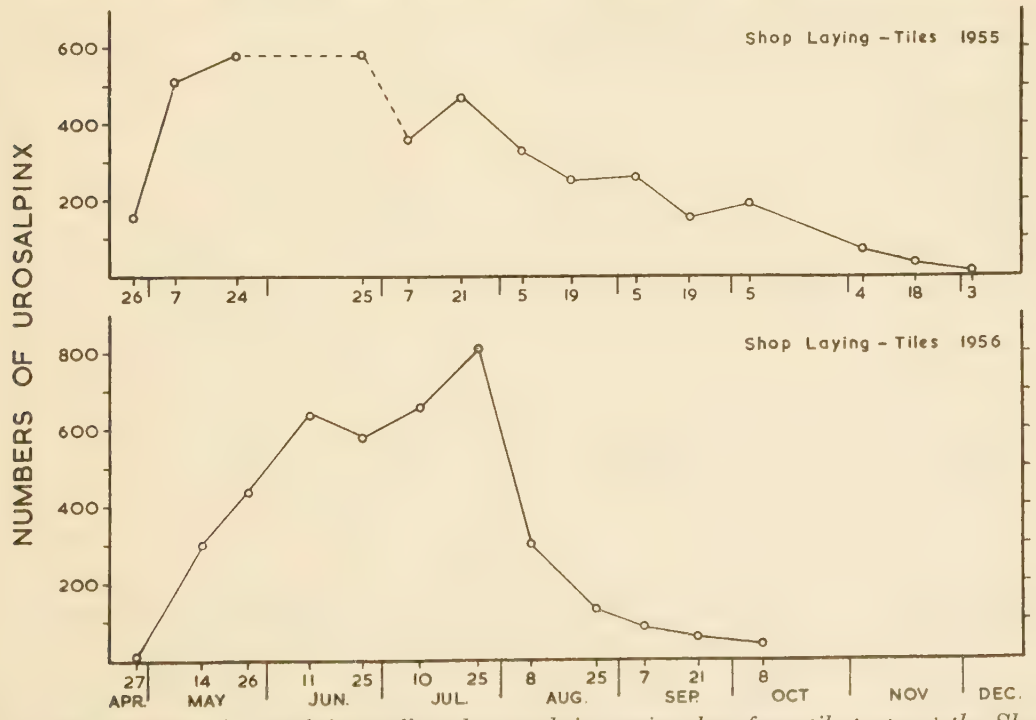

NUMBERS OF UROSALPINX
Shop Laying – Tiles 1955
600
400
200
26 7 24 25 7 21 5 19 5 19 5 4 18 3
Shop Laying – Tiles 1956
800
600
400
200
27 14 26 11 25 10 25 8 25 7 21 8
APR. MAY JUN. JUL. AUG. SEP. OCT NOV DEC.

Fig. 25. *Numbers of* Urosalpinx *collected on each inspection date from tile traps at the Shop Laying, River Roach,* 1955 *and* 1956. *Broken lines indicate abnormal catches when the previous normal date of inspection was missed (see text).*

capsules were removed by trapping and dredging. 200 tiles (Rows A–D, Fig. 7) were retained in the same position for four years, with the following results:—

Year	*Tingles captured*	*Number of capsules taken*
1953	1,077	not recorded
1954	3,752	16,100
1955	2,369	not recorded
1956	1,119	4,960

In 1953, tiles were laid after the beginning of the season, and catches were reduced by the newness of the tiles. The reduction in catches between 1954 and 1956 is attributed to the effects of trapping on the shoreward-moving part of the population.

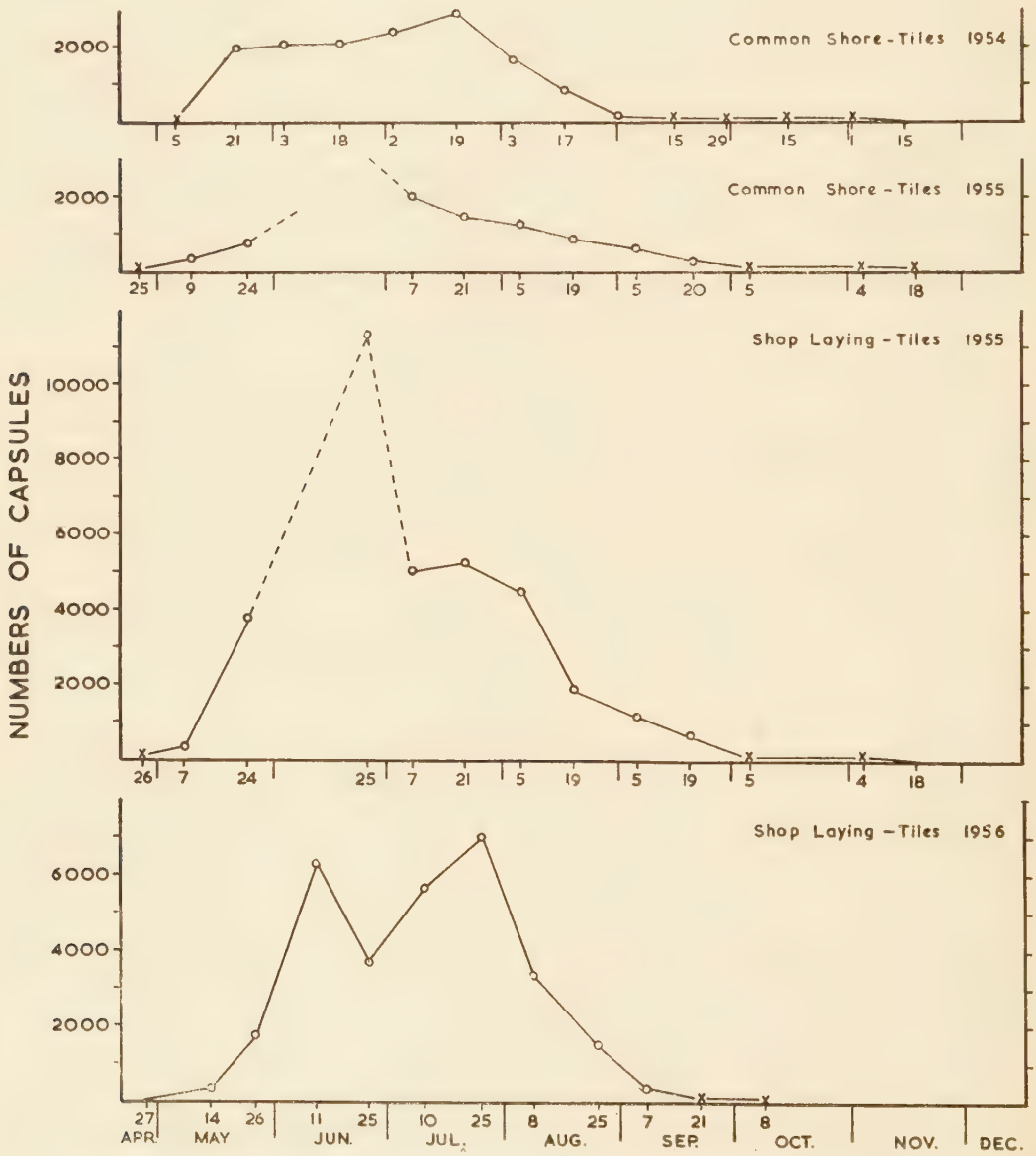


Fig. 26. *Numbers of* Urosalpinx *capsules collected on each inspection date from tile traps at the Common Shore*, 1954 *and* 1955, *and the Shop Laying*, 1955 *and* 1956. *Broken lines indicate abnormal catches when the previous normal date of inspection was missed* (*see text*). *Points marked* (x) *indicate capsules present, but less than* 100.

The capture of 16,000 tingles on traps at the Common Shore and Shop Laying in two years (1955 and 1956) represents, without making allowance for repopulation, the clearing of adult tingles from approximately 7,000 sq. m. of oyster ground. The removal of 64,000 capsules during the same period from traps at the Shop Laying alone represented the destruction of over 700,000 hatching juveniles, and will have reduced the repopulation rate considerably. During the summer, about 65% of the tingles captured are females. Each tingle has been estimated to be capable, under natural conditions, of destroying 40 oyster spat each year.

Two hundred and twenty-five tiles inspected fortnightly at the Shop Laying, yielded 3,900 tingles and 34,000 capsules in 1955, and 4,050 tingles and 30,200 capsules in 1956 (Figs. 25 and 26). All but a fraction of these were taken in only eight visits during each year. It takes two men a half-hour at most to examine 200 tiles, so that the annual catch of 4,000 tingles represents only eight man-hours. This may be compared with the catch of only 250 tingles taken in 4 hours by a boat with a crew of six using two power dredges. The dredges, however, in the same time caught more than twice the year's catch of spawn from the tiles.

At Cole's (1956) estimate that the removal of each tingle represents a saving of 2s.6d., the annual saving at Shop Laying alone from the use of tiles would amount to £500. This is a conservative estimate and does not include (a) spawn removed, and (b) the enormous potential saving by preventing the captured tingles from feeding for several further years, and from producing numerous offspring.

In 1955, of a total of 12,176 *Urosalpinx* removed from the Common Shore and the Shop Laying, 8,600 were taken by traps. The small number of 35 tiles placed at L.W.O.S.T. in Tollesbury Fleet, River Blackwater (by courtesy of Mr. W. A. Bentley and inspected by Mr. C. Pullen) yielded 638 tingles in 1955.

These studies have demonstrated that on oyster grounds where a fair proportion of the tingle population moves on to the shore, tiles can be used economically and efficiently. The tiles should be allowed to overwinter on the shore to remove newness; they should be placed in rows near L.W.O.S.T. and inspected regularly. Such tiles would be useful for screening oysters cultivated on the shore. To avoid damage by treading, a space clear of oysters should be left around the traps. Alternatively, boards and sacking ('pattens') strapped to the feet could be used to advantage, as at West Mersea and Brightlingsea during the cultivation of Portuguese oysters.

5. DISINFECTION OF OYSTERS

The obvious difficulty confronting the use of molluscicides lies in the close systematic relationship between predator and prey. The ability of the oyster to close its valves against unfavourable elements is matched in a degree by the action of the operculum in *Urosalpinx*, which can prevent desiccation during exposure for a number of days. A modest start was made by tackling the problems of disinfecting oysters intended for transportation from areas within the distribution of *Urosalpinx*, to those at present free.

The contents of spawn capsules immersed in solutions of methylene blue are quickly stained. Staining of embryos by potassium permanganate solution occurs within five minutes, showing that chemicals can penetrate the capsules within a short time.

(a) FRESH WATER

Adult tingles survived after 18 hours immersion in cold fresh water. 40% of tingles immersed in fresh water at 43°C. for 1 minute, survived, but none survived immersion in fresh water at 54°C., for 5 minutes. Ten oysters, covered by numerous fresh capsules containing eggs, were immersed in fresh tap-water for 1 hour. The oysters were unaffected by this treatment, but no subsequent development of the eggs took place. Normal development proceeded in the control experiment. One month later, oysters from the control experiment bearing capsules containing veligers, were immersed in fresh water for 6, 10, 20, 30, 45 and

60 minutes respectively and replaced in running sea-water. Juveniles hatched from some capsules on all the oysters; the oysters were unaffected. Evidently fresh water will kill the egg, but not subsequent stages. This is important when planning dipping experiments in chemicals, which should be used in sea-water solutions first. The egg stage has been shown previously (Hancock, 1956) to be killed by temperatures below 5°C., and seems to be a point of weakness in the life history of *Urosalpinx*.

(b) REDUCED SALINITY

Experiments in which oysters and tingles were kept in waters of reduced salinities at various temperatures in the laboratory showed that the survival period was usually longer in tingles than oysters, so that this would not be a suitable method for disinfection. It did show, however, that oysters survived a maximum of 9 days immersion in fresh water, and tingles 11 days.

(c) FORMALIN

Spawn, oysters and tingles were dipped in 0·25% Formalin for 1½ and 2 hours, and placed in cages in the river. The adult tingles survived this treatment but the oysters showed 20–30% mortalities. The spawn was not examined for more than two months, and although almost 70% of the capsules remained undeveloped, the remainder were empty. It has since been shown that the opercula of dead capsules containing already developing embryos are lost in a period not much longer than the hatching period, so that all the capsules may have been killed. In view of the oyster mortality this line of attack was not pursued.

(d) POTASSIUM PERMANGANATE

This was tried as a cheap, easily obtainable chemical, lethal to certain organisms. Adult tingles and oysters covered by tingle spawn were immersed for 1 hour in a 0·15% solution of permanganate in sea-water. Penetration was very quick, and the albuminous fluid and embryos, but not the eggs, became stained. Oysters and tingles were unaffected, and development of nearly all the eggs in each capsule continued, even though the embryos had become stained by permanganate.

(e) CHLOROS AND PHENOL

A similar procedure was adopted using for 1 hour (a) a solution of Chloros (*ca.* 10% Cl_2) in sea-water (2 ml. in 5 litres) and (b) a 0·15% solution of Phenol in sea-water. Oysters, tingles and spawn survived. Chloros was chosen since it is already used in the purification of oysters from pollution, and Phenol has been used with some success for killing *Polydora* infesting oysters (G. D. Waugh, personal communication).

(f) COPPER SULPHATE

Oysters, *Urosalpinx* and its spawn, and *Crepidula* were placed for varying periods in solutions of copper sulphate of different strengths in sea-water, and then returned to running sea-water in the laboratory (Tables 24 and 25). *Urosalpinx* spawn was killed after immersion for 30 minutes in solutions of strengths 1 : 200 to 1 : 2000 but not in 1 : 4000. The oysters seemed unaffected by dipping and usually grew normally in subsequent weeks. *Crepidula* usually died in all concentrations used, though there was one case of anomalous survival in one of the weaker (1 : 2000) solutions. The limpets seemed to be filtering quite actively during immersion. Death followed more rapidly after immersion in the stronger solutions. Other fouling organisms such as *Ascidiella* and *Ciona* were killed in solutions of 1 : 200—other strengths were not used against them. Confirmatory results were obtained by repeating these experiments with suitable controls and placing the oysters on the shore. Korringa (1950) recommended immersion in a dilute solution of copper sulphate (1 : 5000) for 2 hours for the killing of young *Crepidula* settled on oyster spat collectors.

Table 24: *Effects on* Urosalpinx *and spawn, Oysters and* Crepidula, *after dipping in copper sulphate solutions in the laboratory*

Strength of $CuSO_4$ solution	*Period of immersion*	Urosalpinx	*Spawn*	*Oysters*	Crepidula
1 : 200 sea-water	1 hour	None survived	None survived	Unaffected	Not used
1 : 200 sea-water	30 mins.	2 out of 5 died	None survived	Unaffected	None survived
1 : 200 sea-water	30 mins.	3 out of 5 died	None survived	Unaffected	None survived (9 dipped)
1 : 200 sea-water	15 mins.	1 out of 5 died	– – – – – – not dipped – – – – – –		
1 : 400 sea-water	30 mins.	All survived	None survived	Unaffected	None survived
1 : 1000 sea-water	30 mins.	All survived	None survived	1 out of 6 died	None survived
1 : 2000 sea-water	30 mins.	All survived	None survived	Unaffected	7 out of 8 dead
1 : 4000 sea-water	30 mins.	All survived	Survived	Unaffected	None survived
1 : 200 fresh water	30 mins.	1 out of 5 died	None survived	Unaffected	None survived (7 dipped)
1 : 500 fresh water	30 mins.	1 out of 5 died	None survived	Unaffected	2 survived (4 dipped)
1 : 1000 fresh water	30 mins.	All survived	None survived	Unaffected	None survived (9 dipped)
1 : 2000 fresh water	30 mins.	All survived	None survived	Unaffected	3 survived (5 dipped)

Embryos in *Urosalpinx* capsules returned immediately to sea-water after dipping for periods of 1, 2 and 5 minutes in copper sulphate solution (1 : 200) in sea-water, survived, but all were killed by 15 minutes immersion. Engle (1941, *cit.* Carriker, 1955) reported the effective killing of all stages of embryos in the laboratory, without harming oysters, by dipping the capsules in a solution of $CuSO_4$ (1 : 200) in sea-water for 1 minute. Weaker solutions (1 : 300) did not kill all the embryos.

To ensure a time-margin of safety for oysters, 250 were dipped in a copper sulphate solution (1 : 200) in sea-water for 1 hour and placed on the shore near low-water-mark. There was no significant mortality during the following two months, and normal growth took place. Some adult *Urosalpinx*, however, survived even after 4 hours in a 1 : 200 solution in the laboratory (Table 25).

Walne (1956) dipped tile collectors in copper sulphate solution (1 : 250) and dried them for 1 to 2 hours before returning them to the water. This was effective for killing competitors, while oyster spat survived well in both methods. This method has been modified by placing oysters with *Urosalpinx* spawn and adult tingles in copper sulphate solution (1 : 200) in sea-water for 1–3 minutes and leaving them out of water for extended periods before replacing in sea-water. In the laboratory, oysters survived well and *Urosalpinx* spawn died after dipping for 1 and 3 minutes respectively, and exposing to air for 2 hours. In the field, oysters survived well after 2 minutes dipping and placing in damp sacks for 2, 21 and 45 hours, before replacing in sea-water. Most adult tingles survived each dipping.

Preliminary experiments have shown that there is a high mortality among oyster spat in copper sulphate solution (Table 26), at least in warmer weather, while barnacles are less

Table 25: *Effects on* Urosalpinx *and oysters 4 weeks after dipping in copper sulphate solution (1 : 200) in sea-water in the laboratory in April, 1957 (Temperature: 12–13°C.)*

Period of immersion	Urosalpinx		*Oysters*	
	Live	*Dead*	*Live*	*Dead*
1 hour	9	1	4	1
2 hours	7	3	4	1
3 hours	1	9	4	1
4 hours	2	8	4	1
5 hours	0	10	4	1

Table 26: *Effects on oyster spat,* Crepidula *spat and barnacles after dipping shells bearing them in copper sulphate solution* (1 : 200) *in sea-water,* (A) *for* 30 *minutes and returning to sea-water, and* (B) *for* 3 *minutes followed by exposure to air for* 2 *hours before returning to sea-water;* (C) *were untreated*

Experiment	*Oyster spat*		Crepidula *spat*		*Barnacles*	
	Live	*Dead*	*Live*	*Dead*	*Live*	*Dead*
A	2	56	0	10	141	136
B	2	35	0	3	308	158
C	61	1	12	0	Numerous	0

easily affected. By Walne's method, the oyster spat survived, but they were removed at once from the copper sulphate solution. This would probably not be as effective against *Urosalpinx* spawn. Additional experiments are required.

It seems that copper sulphate can be used effectively to kill *Urosalpinx* spawn, but so far no practical method has been found for killing adult *Urosalpinx* in the presence of oysters

6. A SYSTEM OF CONTROL

Although normal dredging is not the most efficient method of catching tingles, it is the basic process of oyster cultivation in operation throughout the year, and the many tingles caught in this way should be carefully saved. The best catches of tingles and spawn are obtained from May to August, however, when native oysters are out of season and dredging is at a minimum. Dredging, particularly for spawn, should therefore be included in the programme of summer cultivation. Tingles caught should be exposed for more than one week, and, for safety, are best dumped on the saltings. Spawn should be scraped off oysters or other objects and killed in hot water or dried out. Where the proportion of small shell or 'shram' and small 'singled' brood oysters in the catch is not too high, a tingle dredge may be used to advantage, and the catch taken ashore unsorted for drying. On such a ground, a useful aid to culling would be a movable tray made of one-inch-square mesh heavy wire screening. During sorting of the catch, tingles and small shell would fall into a container below, and the rest of the catch could then be tipped overboard by tilting the tray.

Roofing-tiles set at L.W.O.S.T. are the most efficient traps known for tingles, and they should be arranged as suggested (p. 56) if large catches are to be obtained. They should be inspected at least once a fortnight, and are best left underwater for a period of years.

Larger tiles and 'bouquets' of tiles may be attached to a line and set below L.W.O.S.T. on oyster layings with shores which, due perhaps to deposits of mud, adjacent sea-walls etc., are free from tingles. The trap-line may be inspected from a boat or by wading at spring tides.

Until a method for the complete destruction of *Urosalpinx* can be devised, such mechanical means of limiting the population should be vigorously employed. It has been demonstrated that in this way numbers can be reduced in a few years. Even on oyster grounds where numbers are few, each tingle removed represents a great saving of oyster spat and brood in the future. It has been shown that the density of tingles on one oyster laying has increased from just a few to ten thousand per acre in fifteen years. This is not surprising since, if all hatching young survived, the number of descendants of one pair of tingles by normal breeding would in five years exceed seven million. There is obviously a high mortality rate amongst young tingles. There is, however, no free-swimming larval stage, and fully formed young tingles emerge from the capsules. The chance of survival is thereby much increased; but the rate of spread is much slower than that of a species with free-swimming larvae. The distribution of *Urosalpinx* in England has so far shown no significant extension from its original introduction, except by the agency of the oysterman. Experience has shown that the transport of oysters from areas within the distribution of *Urosalpinx* for relaying on oyster grounds at present free from the pest, may have serious consequences. It would be impossible, even by minute inspection, to eliminate every tingle or spawn capsule from a large consignment of oysters. The overlooking of only two tingles, or a little spawn, could lead to heavy losses of oyster spat and oysters, and to the necessity for intensive control measures within a short time.

The British native oyster industry needs for its survival a good settlement of oyster spat. Each *Urosalpinx* destroyed will be a substantial contribution towards increased oyster production. The measures of control so far devised, although incomplete, would, if generally employed, bring about a substantial reduction in the numbers of this pest.

X. SUMMARY

1. The American whelk tingle, *Urosalpinx cinerea* (Say), introduced into Britain with American oysters about half a century ago, has only slightly increased its range, but great increases in density have been recorded.

2. During spring and summer each year, large numbers, including a high percentage of females, migrate into the intertidal zone. A reverse migration later in the year was demonstrated by means of marked tingles.

3. Winter hibernation occurs generally below 7°C., and as the water temperature rises, feeding commences at 9–10°C., followed by spawning at 11–12°C.

4. Laboratory and field observations showed that *Urosalpinx* feeds preferentially on oyster spat, and under natural conditions each tingle can be expected to consume about 40 spat during a normal feeding season. The feeding rate increased with temperature.

5. Female tingles grow faster than males; both reach maturity during their second year. Growth data were found to fit von Bertalanffy's growth equation.

6. The size-distribution of *Urosalpinx* showed considerable variation even between closely situated localities. The largest tingles deposit the biggest capsules, which contain most eggs. This behaviour requires consideration when sampling.

7. Maximum spawning occurs annually from May to July, but may extend from April to November. Only a small percentage of eggs fails to develop normally. Embryos hatch as fully-formed juveniles, capable of attacking small oyster spat immediately.

8. Adult tingles survived exposure to air for periods of up to eight days. Survival time was inversely related to temperature.

9. The habits of *Urosalpinx* have been examined with reference to present methods of oyster cultivation, and to the design of a programme of control. Tingle dredges and wire

bag traps were used with little success, but curved roofing-tiles placed at L.W.O.S.T. caught many tingles and reduced the population considerably. Such traps are simple and cheap to use, but spawn may be taken most successfully by dredging.

10. If oysters from the east coast of England were transferred to areas at present free from *Urosalpinx*, there would be a serious risk of further spread of the pest.

XI. REFERENCES

Bailey, N. T. J. (1951). On estimating the size of mobile populations from recapture data. *Biometrika*, **38,** 293–306.

Bertalanffy, L. von (1938). A quantitative theory of organic growth (Inquiries on growth laws II). *Human Biology*, **10,** 181–213.

Brooks, W. K. (1879–1880). Preliminary observations on the development of the marine prosobranchs. *Studies Biol. Lab. John Hopkins Univ., Chesapeake Zool., Lab. Sci. Results* 1878, 121–42.

Bullock, T. H. (1953). Predator recognition and escape responses of some intertidal gastropods in presence of starfish. *Behaviour*, **5,** 130–42.

Carriker, M. R. (1943). On the structure and function of the proboscis in the common oyster drill, *Urosalpinx cinerea* Say. *J. Morph.*, **73,** 441–98.

— (1955). Critical review of biology and control of oyster drills *Urosalpinx* and *Eupleura, U.S. Fish and Wildlife Service. Spec. Sci. Rep., Fish.* No. 148.

Cassie, R. M. (1954). Some uses of probability paper in the analysis of size frequency distributions. *Aust. J. Mar. Freshw. Res.*, **5,** 513–22.

Cole, H. A. (1942). The American whelk tingle, *Urosalpinx cinerea* (Say), on British oyster beds. *J. mar. biol. Ass. U.K.*, **25,** 477–508.

— (1951). The British oyster industry and its problems. *Cons. int. Explor. Mer. Rapp. et Proc. Verb.*, **128,** 7–17.

— (1956). Oyster cultivation in Britain. *H.M.S.O., London.*

Cole, H. A. and Hancock, D. A. (1955). *Odostomia* as a pest of oysters and mussels. *J. mar. biol. Ass. U.K.*, **34,** 25–31.

Engle, J. B. (1941). Further observations on the oyster drills of Long Island Sound, with reference to the chemical control of embryos. *Conv. Addr., Natl. Shellfish Assoc., Atlantic City, N.J.*

— (1942). Growth of the oyster drill, *Urosalpinx cinerea* Say, feeding on four different food animals. *Anat. Rec.*, **84,** 505.

Federighi, H. (1931). Studies on the oyster drill (*Urosalpinx cinerea*, Say). *Bull. U.S. Bur. Fish.*, **47,** 85–115.

Fraser, J. H. (1931). On the size of *Urosalpinx cinerea* (Say) with some observations on weight–length relationship. *Proc. Malacol. Soc. Lond.*, **19,** 243–54.

Fretter, V. (1941). The genital ducts of some British stenoglossan prosobranchs. *J. mar. biol. Ass. U.K.*, **25,** 173–211.

Galtsoff, P. S., Prytherch, H. F. and Engle, J. B. (1937). Natural history and methods of controlling the common oyster drills (*Urosalpinx cinerea* Say and *Eupleura caudata* Say). *U.S. Bur. Fish., Fish. Circ.*, No. 25.

Glancy, J. B. (1954). Oyster production and oyster drill control. *Proc. Natl. Shellfish Assoc.*, **44,** 61–66.

HANCOCK, D. A. (1954). The destruction of oyster spat by *Urosalpinx cinerea* (Say) on Essex oyster beds. *J. Cons. int. Explor. Mer*, **20**, 186–96.

— (1955). The feeding behaviour of starfish on Essex oyster beds. *J. mar. biol. Ass. U.K.*, **34**, 313–31.

— (1956). The structure of the capsule and the hatching process in *Urosalpinx cinerea* (Say). *Proc. zool. Soc. Lond.*, **127**, 565–71.

HARDING, J. P. (1949). The use of probability paper for the graphical analysis of polymodal frequency distributions. *J. mar. biol. Ass. U.K.*, **28**, 141–53.

HASKIN, H. H. (1935). Investigations on the boring and reproduction activities of the oyster drills *Urosalpinx cinerea* Say and *Eupleura* sp. *Rep. U.S. Bur. Fish., Wash.* (Unpublished).

— (1940). The role of chemotropism in food selection by the oyster drill, *Urosalpinx cinerea* Say. *Anat. Rec.*, **78**, 95.

— (1950). The selection of food by the common oyster drill, *Urosalpinx cinerea* Say. *Proc. Natl. Shellfish Assoc.*, 1950, 62–8.

KORRINGA, P. (1950). A review of papers on molluscs presented at the special scientific meeting on shellfish of the International Council for the Exploration of the Sea, Edinburgh, 10th October 1949. *J. Cons. int. Explor. Mer*, **17**, 44–59.

LUCAS, C. E. (1947). The ecological effects of external metabolites. *Biol. Rev.*, **22**, 270–95.

MISTAKIDIS, M. N. (1951). Quantitative studies of the bottom fauna of Essex oyster grounds. *Fish. Invest.*, Ser. 2, **17**, No. 6.

MISTAKIDIS, M. N. and HANCOCK, D. A. (1955). Reappearance of *Ocenebra erinacea* (L.) off the east coast of England. *Nature, Lond.*, **17**, 734.

MOORE, H. B. (1936). The biology of *Purpura lapillus*. I. Shell variation in relation to environment. *J. mar. biol. Ass. U.K.*, **21**, 61–89.

MOORE, H. F. (1898). Oysters and methods of oyster culture. *Rep. U.S. Comm. Fish & Fish.*, 1897.

NEEDLER, A. W. H. (1941). Oyster farming in Eastern Canada. *Bull. Fish. Res. Bd. Can.*, No. 60.

NELSON, J. R. (1931). Trapping the oyster drill. *Bull. N. J. Agric. Exp. Sta.*, No. 523.

NELSON, T. C. (1922). The oyster drill: a brief account of their life history and possible means of combating them. *Appendix Rep. Biol., N. J. Sta. Bd. Shellf., Nov.* 1922.

ORTON, J. H. (1927). The Habits and Economic Importance of the Rough Whelk-Tingle (*Murex erinaceus*). *Nature, Lond.*, **120**, 653–4.

— (1929). Habitats and feeding habits of *Ocinebra erinacea*. *Ibid*, **124**, 370.

— (1930). On the oyster-drills in the Essex estuaries. *Essex Naturalist*, **22**, 298–306.

— (1937). Oyster Biology and Oyster Culture. *Arnold: London.*

ORTON, J. H. and AMIRTHALINGAM, C. (1929). The oyster drills on English oyster beds. *Nature, Lond.*, **124**, 298.

ORTON, J. H. and LEWIS, H. M. (1931). On the effect of the severe winter of 1928–1929 on the oyster drills (with a record of five years' observations on sea temperatures on the oyster beds) of the Blackwater Estuary. *J. mar. biol. Ass. U.K.*, **17**, 301–13.

ORTON, J. H. and WINCKWORTH, R. (1928). The occurrence of the American oyster pest *Urosalpinx cinerea* (Say) on English oyster beds. *Nature, Lond.*, **122**, 241.

POPE, T. E. B. (1910–11). The oyster drill and other predatory mollusca. *Rep. U.S. Bur. Fish., Wash.* (Unpublished).

SIZER, I. W. (1936). Observations on the oyster drill with special reference to its movement and to the permeability of its egg case membrane. *Rep. U.S. Bur. Fish., Wash.* (Unpublished).

SMITH, G.F.M. (1940). Factors limiting distribution and size in the starfish. *J. Fish. Res. Bd. Can.*, **5**, 84–103.

STAUBER, L.A. (1938). Oyster drill control in Delaware Bay. *Conv. Addr., Nat. Shellf. Assoc., Providence, R.I.*

— (1943). Ecological studies on the oyster drill, *Urosalpinx cinerea*, in Delaware Bay, with notes on the associated drill, *Eupleura caudata*, and with practical consideration of control methods. *Rep. Oyster Res. Lab., N.J.* (Unpublished).

STAUBER, L.A. and LEHMUTH, G.M. (1937). Costs and profits in oyster drill control. *Bull. N.J. Agr. Exp. Sta.*, No. 624.

STEHOUWER, H. (1952). The preference of the slug *Aeolidia papillosa* (L.) for the sea anemone *Metridium senile* (L.). *Arch. néerl. Zool.*, **10**, 161–70.

TANAKA, Y. (1950). Injuring mechanisms of the oyster drill (*Purpura clavigera*) to young oysters (*Ostrea gigas*). *Bull. Jap. Soc. Sci. Fish.*, **15**, 447–57.

THAMDRUP, H.M. (1938). The van Veen bottom-grab. *J. Cons. int. Explor. Mer*, **13**, 206–12.

WALNE, P.R. (1956). Destruction of competitive organisms on artificial oyster-spat collectors. *J. Cons. int. Explor. Mer*, **22**, 75–6.

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